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HABITS AND BIOLOGICAL RELATIONSHIPS OF THE PRIMARY PARASITES APHIDIUS TESTACEIPES CRESSON AND PRAON AGUTI SMITH AND THE HYPERPARASITE ASAPHES FLETCHERI CRAWFORD

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INTRODUCTION

The problems confronting humanity due to insects and other pests are unlimited. Even in the days of oriental prosperity, there were frequent encounters between man and insect pests. The methods employed to overcome these pests were, however, simple and less technical. The progress of science since has brought many improvements in the application of biological control and other methods of control as well. Today, biological control occupies a place alongside the other methods of control: mechanical, ecological, chemical and legislative.

The practice of biological control, according to Sweetman (1936), owes its origin to the fact that numerous injurious insects and plants are themselves attacked by parasitic and predaceous species. The presence of entomophagous parasites is one of the many advantages that nature has afforded man in the field of insect control. The beneficial insects not only help to protect the daily needs of man but also present interesting examples of intricate behavior.

Insect control through biological methods has been subject to failures as well as successes (Sweetman, 1935). The selection of examples of failures and successes depends

somewhat upon the individual viewpoint. Further, analysis of the results of the many existing attempts through biological control is very difficult primarily due to the complexity of the problem. This encumbrance has often resulted in vague conclusions, and consequently, some introductions of parasitic and predaceous organisms have produced unexpected failures. For example, only two parasites out of ten that were introduced into the United States between 1911 and 1934 to combat the alfalfa weevil have become established. One of these, Bathyplectes curculionis (Thoms.), has a wide distribution and frequently parasitizes a high percentage of larvae, but has materially reduced the host population level only in the coastal regions of California (Michelbacher, 1943).

The difficulty in the execution and interpretation of biological control methods is due not only to the great number of factors involved in a closely adjusted host-parasite relationship but also to the complexity of interactions of these factors. Some of these factors are advantageous while others are limitational to the organisms involved. Taking a primary parasite species as an example, two of the greatest advantages that it may possess are a higher reproductive potential and a shorter life cycle than its host species. One important limitation that the same primary

parasite species may face is frequent dependence upon a particular stage of a specific host for completion of the life cycle. Secondly, the same individual host or even the same stage of the host species may be a target for attack of other primary parasite species. If this happens, competition frequently occurs between the two primary parasite species, and the result is usually unfavorable for one or both species of primary parasites. Further, the question of hyperparasites is a matter of great concern. Practically no primary parasite species escapes the attacks of hyperparasites. The hyperparasites, in general, being less discriminatory than the primary parasites in the selection of hosts, have a wide range of choice of hosts. However, the hyperparasites are also apt to face the same interfering problems, both physical and biotic, in their life as those faced by the primary parasites. For instance, a secondary parasite may be attacked by a tertiary parasite, and a tertiary, in turn by other parasites.

From the above treatment, it is obvious how complex the subject of parasitism can be under varying conditions. In the present study, the interrelationships of the aphid hosts, the primary parasites (Aphidius testaceipes Cresson and Praon aguti Smith) and the hyperparasite (Asaphes fletcheri Crawford) are considered in detail. The primary

parasites have, in common, certain prerequisites in their host species. So also has the hyperparasite.

For the sake of convenience, the two primary parasites and the hyperparasite are treated in separate parts. Part I deals with the primary parasites and Part II with the hyperparasite. In the treatment of host-parasite relationships, the influence of certain ecological factors on the various phases of the life histories of the three species has also been evaluated where feasible.

PART I

THE PRIMARY PARASITES APHIDIUS TESTACEIPES CRESSON AND PRAON AGUTI SMITH

ANALYSIS OF LITERATURE

The Subfamily Aphidiinae (Braconidae)

Earlier writers considered Aphidiinae a distinct family but it is now placed as a subfamily of the Braconidae (Muesebeck et al, 1951). Although the Aphidiinae differ considerably in structure from typical Braconidae, the resemblance in most structural details is sufficient to establish a relationship. According to Smith (1944), "the fact that all segments are freely flexible, separates this group from all others of the family, while the wing venation is for the most part somewhat more simple and attenuated than that of other Braconidae". The following description of the subfamily was given by Smith (1944): "The Aphidiinae are small, slender-bodied insects, the largest species measuring not more than four or five millimeters in length. The head is either transverse or quadrate as seen from above and distinctly margined posteriorly; i.e., with sharp carinae separating the occiput from the cheeks, temples and vertex; the temples are convex and usually narrow; the mandibles are triangular, somewhat curved, and bidentate at the apex; maxillary palpi often as long as the head and two to four segmented, labial

palpi one to three segmented and short. The antennae are filiform, many segmented, the scape and pedicel short and subglobose. The prothorax is short, mesonotum gibbous, the notaulices present or absent, the mesoscutellum convex, not large; mesopleura large and occupying most of the side of the thorax. The metathorax is very short; propodeum short, usually convex though sometimes nearly flat or excavated posteriorly, generally carinate (bearing carinae) but without carinae in the genus Praon and with the dividing carinae often indistinct or absent in some species of the other genera. The legs are rather long and slender as in other Braconidae.... The stigma is triangular to nearly lanceolate; there are usually two complete basal or median cells and the second discoidal cell is usually though not always complete. The rest of the neuration varies greatly. The radial cell is rarely complete and may be entirely effaced. There may be three, two, or one, or no cubital cells. When three cubitals occur (Ephedrus) the first discoidal and first cubital are separated, and cubital cross veins and recurrent veins are present. When but two cubitals are represented the first cubital and first discoidal are confluent and recurrent vein complete or nearly so, (Aphidius, in part, & Monoctonus), or the recurrent vein is absent or incomplete (subgenera Lysiphlebus & Lysaphidus). If only

one cubital cell is present the cubital cross veins are absent and the first abscissa of cubitus is present with the recurrent vein either present or absent (Praon); in case of no cubital cells, cubitus, the cubital cross veins, and the recurrent veins are entirely effaced (Trioxys, Diaeretus). The subdiscoidal vein is usually interstitial, though occasionally arising from the middle of the second discoidal cell, and is never very distinct. The female abdomen is petiolate or subpetiolate, usually long and lanceolate but occasionally short and ovate (when lanceolate the apex is compressed laterally), the dorsal sutures being flexible allowing it to be freely bent beneath the thorax; the ovipositor is rarely exserted. The male abdomen is usually short and ovate or spatulate".

The Genera

The genera erected in the subfamily Aphidiinae were many. The origin and validity of such genera have been thoroughly examined by Gahan (1911) and the account given by him is as follows: "Twenty-five generic names have been used in this group. Aphidius was described by Nees von Esenbeck in 1818. In 1833 Haliday characterized Monoctonus, Ephedrus, Praon, Trionyx, and Trioxys. Wesmael added Elassus in 1835. In 1840 the name Toxares was proposed by Haliday. Foerster in 1862 published a

table of genera of the Aphidiinae in which he included six new genera, viz: Lysiphlebus, Diaeretus, Paralipsis, Coelonotus, Lipolexis, Adialytus and Aclitus. He at the same time fixed the types for all of his own as well as some of the previously described genera. Theracmion was described by Holmgren in 1872 without indicating to what group of Braconidae it belonged. In 1881 Provancher described Artropus and Copelus as new genera in this group, and followed these in 1886 with descriptions of Aphidaria, Neuropenes, Ropronia, Radiolaria and Scotioneurus. Rondani, an Italian writer introduced the name Misaphidius in 1874. Thompson in 1895 accidentally introduced Coclonotus, and a year later appeared Marshall's description of Dyscritus. The last of the twenty-five, Protaphidius, was proposed by Ashmead in 1900 as a substitute for Coelonotus which he stated is preoccupied.

"Haliday's names were all proposed as sub-genera of Aphidius, but with the exception of Trionyx all are now recognized and accepted as generic names. Trionyx was found to be preoccupied in Reptilia and the name Toxares substituted for it. Wesmael's description of Elassus is plainly that of an Ephedrus and the name has been recognized as a synonym by most writers since 1840. Holmgren's genus Theracmion which is catalogued as an Ichneumonid by Dalle Torre is synonym of Aphidius according to A. Roman

who has examined the types.

"Regarding Foerster's genera there has been much difference of opinion. In the opinion of the writer Lysiphlebus, Diaeretus and Paralipsis are entitled to rank as good genera. The sole character given by Foerster to distinguish Coelonotus from Aphidius is that the propodium (mesonotum) is hollowed out. Among the species possessing the typical wing venation as well as all the other characters of Aphidius is found considerable variation in the shape of the propodium, some species having it quite convex, others nearly flat, while in still others it is sunken or concave. In view of this fact it seems best to accept Marshall's treatment of Coelonotus as a synonym of Aphidius. Lipolexis and Adialytus are founded upon characters of minor importance and which are subject to considerable variation making it impossible to separate them from Diaeretus.... Aclitus which Foerster separated from Aphidius on the ground that the propodium is unareolated and the radius somewhat elongated enclosing two-thirds of the radial cell, is in my opinion untenable since the length of radius is subject to considerable variation in species having the propodium distinctly areolated and in at least one species of Aphidius having this vein of normal length the areolation of the propodium is practically effaced. Paralipsis, Lysiphlebus and Diaeretus are recognizable by the characters given by

Foerster and seem to be distinct enough to stand as good genera.

"Of the genera placed in this group by Provancher, Ropronia, Copelus, and Artropus were later transferred by their author to other groups the two former to the Proctotrypidae and the latter to Formicidae. Radiolaria is placed in the Dacnusinae by Ashmead. Aphidaria was erected for a species which the author later correctly designated as Praon. This should have disposed of the genus but Provancher proceeded to apply the name to another species described by him. This new species, however, proved to be a Lysiphlebus so that the genus Aphidaria is happily disposed of.

Scotioneurus originally included two species. Of these one is an Ephedrus and the other does not belong to the Aphidiinae at all if one may judge by the figure of the wing given by the author. Unfortunately the types of the latter species could not be secured.

"Three species were originally included under Misaphidius. Judged by the figures given by the author of the genus two of these fall in Diaeretus while the other appears to be a Lysiphlebus. Coclonotus is obviously a misprint for Coelonotus, as pointed out by Dalle Torre. Protaphidius being a substitute name for Coelonotus becomes a synonym of Aphidius".

Key to Genera

The concept of generic groups of Aphidiinae as proposed by Gahan (1911), has in general been adopted by later authors like Smith (1944) and Muesebeck *et al* (1951). The key presented here is quoted from Smith (1944).

1. Fore wing with less than three cubital cells. 2

   Fore wing with three cubital cells . . . . . .Ephedrus Haliday

2(1). First cubital and first discoidal cells confluent, the first abscissa of cubitus absent 3

   First cubital and first discoidal cells separated, the first abscissa of cubitus present. . . . . Praon Haliday

3(2). Forewing with a more or less complete discocubital cell; recurrent vein and/or the cubital cross vein may be partly effaced; at least a stub of cubitus is always present . 4

   Forewing with the recurrent vein, cubital cross vein, and cubital vein entirely effaced. 5

4(3). Ovipositor and ovipositor sheath curved downward; first abscissa of radius nearly perpendicular to the stigma. . . Monoctonus Haliday

Ovipositor and ovipositor sheath straight or curved upward; first abscissa of radius not prependicular to the stigma. . . .*Aphidius* Nees

5(4). Female without prongs on the terminal abdominal sternite . . . . . *Diaeretus* Foerster

Female with prongs on the terminal abdominal sternite. . . . . .*Trioxys* Haliday

The Genus Aphidius Nees von Esenbeck

Distribution and hosts. Various species of parasites belonging to this genus are reported from the Americas, Europe, Africa, Asia, Australia, New Zealand, West Indies, Hawaii, etc.

The hosts are exclusively aphids (Thompson 1953, Muesebeck *et al*, 1951). Some of the important ones are listed below:

Aphis gossypii Glov
Aphis rumicis L
Aphis maidis Fitch
Aphis pomi DeG
Aphis fabae Scop
Aphis forbesi Weed
Aphis neogillettei Palmer
Aphis medicaginis Koch
Brevicoryne brassicae L
Macrosiphum granarium Kirby
Macrosiphum pisi Kalt
Macrosiphum rosae L
Macrosiphum solanifolii Ashm, *Myzus persicae* Sulz
Rhopalosiphum prunifoliae Fitch
Toxoptera graminum Rond etc.

The Genus Praon Haliday

Distribution and hosts. Parasites included in this genus have been reported from Britain, Canada, Czechoslovakia, Formosa, France, Jugoslavia, Mexico, Russia, Switzerland, and the United States.

As in the case of Aphidius, the hosts are exclusively aphids (Thompson 1953, Muesebeck et al, 1951). The most common ones are:

Aphis euonymi F
Aphis infuscata Koch
Amphorophora sonchi Oestl
Anuraphis amygdali Buckt
Brevicoryne brassicae L., Eriosoma lanigerum Hausm
Hyalopterus arundinis F
Macrosiphum cornelli Patch
Macrosiphum granarium Kirby
Macrosiphum pisi Kalt
Macrosiphum rosae L
Macrosiphum formosanum Tak
Macrosiphum sonchi L
Macrosiphum illini H & F
Myzus persicae Sulz
Periphyllus negundinis Thomas
Rhopalosiphum pseudobrassicae Davis

The Parasite Aphidius testaceipes Cresson

Synonymy (from Smith, 1944 and Muesebeck et al, 1951)

Trioxys testaceipes Cresson, 1879 (1880)
Aphidius citraphis Ashmead, 1880.
Adialytus maidaphidis Garman, 1885.
Aphidius flavicoxa Ashmead, 1880.
Aphidaria basilaris Provancher, 1888.
Lysiphlebus piceiventris Ashmead, 1889 (1888).
Lysiphlebus minutus Ashmead, 1889 (1888).
Lysiphlebus eragrostaphidis Ashmead, 1889 (1888).

Lysiphlebus coquilletti Ashmead, 1889 (1888).
Lysiphlebus cucurbitaphidis Ashmead, 1889 (1888).
Lysiphlebus myzi Ashmead, 1889 (1888).
Lysiphlebus gossypii Ashmead, 1889 (1888).
Lysiphlebus abutilaphidis Ashmead, 1889 (1888).
Lysiphlebus persicaphidis Ashmead, 1889 (1888).
Lysiphlebus tritici Ashm, 1889 (1888).
Lysiphlebus baccharaphidis Ashm, 1889 (1888).
Aphidius persiaphis Cook, 1891.
Lysiphlebus crawfordi Rohwer, 1909.

Description

It has previously been noted that Lysiphlebus was given the rank of genus by Gahan (1911). However, Muesebeck et al. (1951) consider it as a subgenus of Aphidius, and this classification is followed in the present work.

Adult. Smith (1944) describes the species as follows:

Female: Length 1.5-2.0. Head shiny; width, 0.48-0.63; facial line, 0.31-0.38; clypeoantennal, 0.10-0.13; interocular, 0.29-0.31; transfacial, 0.22-0.25. Antennae 11- to 13-segmented (usually with 13 segments); first flagellar segment, 0.12-0.13; second flagellar, 0.11.

Thorax smooth; width at tegulae, 0.43-0.53; notaulices faintly indicated at the anterior angles of the mesonotum; propodeum without carinae. Length of stigma, 0.40-0.48; width, 0.12-0.14; metacarpus, 0.27-0.34; first abscissa of radius, 0.15-0.20; second abscissa, 0.10-0.17; cubital cross vein, 0.07-0.11; stub of cubitus, 0.06-0.10.

Abdomen smooth; length of the petiole, 0.31-0.34; width at spiracles, 0.11-0.13. Head black, mouthparts usually yellow, occasionally fuscescent; antennae black or brownish black. Thorax black, smooth, and shining. Wings hyaline, veins and stigma brown or brownish black. Fore-legs, including their coxae yellow; meso- and metathorasic coxae, femora, and tibiae usually though not always fuscous, often nearly clear yellow. Abdomen black or brown black, except the petiole which is usually yellow. Ovipositor sheath black.

"Male: Antennae 14- to 15 segmented, the segments slightly shorter than in the female. Abdomen scarcely longer than the head and thorax, rounded at the apex. Legs and abdomen slightly darker than in the female. Otherwise coloration similar to the female".

In Plate 1 is included a copy of Webster and Phillips (1912) drawing of the adult of this species.

Egg. The mature ovarian egg of A. testaceipes is elongate, oval, and tapers at both ends (Plate 1).

Larva. Clausen (1940) states that the majority of the species of Aphidius have simple caudate larvae with no integumentary spines nor paired caudal processes, and the tail is only slightly spined distally.

The first stage larva of A. testaceipes is elongate and uncurved or but slightly curved as it grows older, and is composed of a large head and thirteen body segments that taper gradually to the posterior end, terminating in an elongate 'tail' (Spencer, 1926). Seurat (1899) suggested that the tail aids in locomotion of the larva or is used to prod about in the tissues of the host to hasten disintegration and release of food for the parasite.
Timberlake (1910) believed it to be a respiratory organ. Spencer (1926) countered the opinion of Seurat by suggesting that, in the first larval stage, as in the embryo, absorption, respiration and excretion are carried out by the ectodermal cells of the parasite by a process of osmosis. Hence,

there is very little need for the larva to move around.

The second stage larva is distinguished from the former by its larger size and by the greater curvature of the body. The tail is larger but more blunt than in the preceding stage. Nutrition and respiration, as in the former stage, are entirely cutaneous, as there is still no connection between the mesenteron and the exterior, and the tracheae have not reached a point of development permitting activity. Part of the excretion may be performed by the Malpighian tubes according to Spencer (1926). The same author found a few scattered spines on the body as well as on the tail, thus contradicting Clausen (1940).

When the larva reaches the third stage the tail is no longer present, the ventral curvature becomes more pronounced, the anal segment is blunt at its apex, the salivary glands reveal activity (Wheeler, 1923; Spencer, 1926). Nutrition, respiration and excretion are carried out as in the previous stage.

In the fourth stage the larva becomes much larger and thicker, the mandibles become well developed, the head and posterior segments become comparatively smaller than the remaining segments of the body. The larva becomes very active at this stage and begins to attack the organs of the host, using the mandibles (Spencer, 1926).

The fifth stage or mature larva, according to the illustrations made by Webster and Phillips (1912), is composed of 15 segments. The body tapers toward the head and the anal segment (Plate 1). The salivary glands become fully functional and the mesenteron takes on massive proportions to accommodate the ingested food (Spencer, 1926).

Pupa. The body of the pupa of A. testaceipes is much more arched than that of the mature larva. It bears two rows of distinct elevations or tubercles on the prothorax, the functions of which are unknown (Webster and Phillips, 1912). The terminal segment is pointed. Imaginal growth buds are visible within the body (Plate 1).

Distribution

This parasite has been reported from the following places: United States, Bermuda, Cuba, Hawaii, St. Croix, Mexico, Brazil, Puerto Rico, Canada, and East Africa.

Hosts

Thompson (1953) and Muesebeck et al (1951) have given an elaborate list of hosts, some of which are:

Anuraphis crataegifoliae Fitch
Anuraphis roseus Baker
Aphis forbesi Weed
Aphis gossypii Glov
Aphis laburni Kalt
Aphis helianthi Monell
Aphis bambusae Monro
Aphis cerasifoliae Fitch
Aphis maidis Fitch
Aphis medicaginis Koch

Aphis rumicis L
Aphis spiraecola Patch
Brevicoryne brassicae L, Capitophorus ribis L
Hysteroneura setariae Thos
Macrosiphum fragariae Koch
Macrosiphum granarium Kirby
Macrosiphum rosae L
Macrosiphum citrifolii Ashm
Macrosiphum cucurbitae Thos
Macrosiphum tanaceti L
Myzus persicae Sulz
Myzus cerasi F
Myzus rhamni Fonsc
Rhopalosiphum padi L
Rhopalosiphum pseudobrassicae Davis
Rhopalosiphum prunifoliae Fitch
Toxoptera graminum Rond
Toxoptera aurantii Fonsc

Since A. testaceipes resembles P. aguti in its development, the general biology is discussed for both species in a later section.

The Parasite Praon aguti Smith

Description

Adult. Smith (1944) gave the following description:

"Female: Length, 2.0. Head, thorax, and abdomen smooth; width of head, 0.39-0.41; facial line, 0.29-0.32; clypeo - antennal, 0.12-0.13; interocular, 0.21-0.25; transfacial, 0.15-0.16. Antennae, 17-to-19 segmented (of 11 specimens 2 had 17, 8 had 18, and 1 had 19 segments in the antennae); first flagellar segment, 0.14-0.16 -- second flagellar, 0.10-0.11.

"Width of thorax at tegulae, 0.29-0.35. Length of stigma, 0.45-0.50 -- width, 0.09-0.12; metacarpus, 0.26-0.32; radius, 0.25-0.29; first abscissa of cubitus, 0.19-0.20; second abscissa of cubitus, 0.29-0.32; recurrent vein complete and distinct.

"Length of petiole, 0.20-0.22; width at spiracles, 0.15-0.18.

"Head piceous; face dark ferruginous to piceus; mouthparts including clypeus yellowish to testaceous. Scape, pedicel, and basal portion of the first flagellar segment yellowish to testaceous, remaining flagellar segments piceous. Thorax not unicolorous, mesosternum yellowish to testaceous; pleurae light ferruginous to testaceous; mesonotum and propodeum ferruginous to piceous. Legs yellowish to testaceous. Abdomen yellowish to testaceous; petiole and following abdominal segment usually lighter than other abdominal segments. Ovipositor sheath black.

"Male: Antennae 19-20 segmented (of three specimens 1 had 19 and 2 had 20 segments in antennae). Head, thorax, and abdomen dark ferruginous to piceous, except the mouthparts and petiole which are light ferruginous. Antennae piceous, except a lighter annulus between the pedicel and first flagellar segment. Legs testaceous."

No specific descriptions of the immature stages of P. aguti were found in the literature by the present author. However, some general information on the morphology of the larval and pupal stages of the genus Praon is available. This information is included below to clarify the points of similarity and dissimilarity between Praon and A. testaceipes. The immature stages of the latter have been treated previously in detail.

As in all Aphidiinae, there are five larval stages in Praon. The most marked morphological differences between the immature stages of Praon and A. testaceipes are exhibited in the first stage larva. The first stage larva of Praon has a 13 to 14 segmented body, tapering posteriorly to a cylindrical appendage which in most species is as long as the preceding segment and heavily spined at its apex. Ventral to this and at right angles to it, there is a pair of

slender, but well sclerotized arms (Timberlake, 1910 and Beirne, 1942). Probably, this whole structure is the one that has been designated as a'bifid tail' by Spencer (1926). Conspicuous integumentary spines are present on all or most of the thoracic and abdominal segments of the first and second stage larvae (Beirne, 1942).

Larval stages beyond the second are very similar to those of other Aphidiinae in general. These stages are characterized by thicker and unspined body without caudal processes.

The pupa (Plate 3), asin A. testaceipes, is whitish when first formed, but later the head, thorax, and antennae become dark blackish-brown. The abdomen is strongly curved (Beirne, 1942).

Distribution

This parasite is reported in North America from Ontario to Virginia and west to Ohio (Muesebeck et al., 1951).

Hosts

Smith (1944) and Muesebeck et al (1951) list the following aphids as hosts:

Macrosiphum pisi Kltb
Macrosiphum rosae L
Macrosiphum solanifolii Ashm

General Biology of A. testaceipes and P. aguti

Hibernation and emergence

Hibernation. Spencer's work (1926) shows that the method of overwintering of aphidiine parasites, on the whole, depends more upon the resistance of the plants on which the aphids multiply than upon the severity of the winter. He further pointed out that, in places where growing conditions are favorable and the plants do not die from cold or maturation, the parasites continue to reproduce and migrate to other suitable localities. He also suggested that the parasites overwinter in greenhouses. According to Webster and Phillips (1912), A. testaceipes hibernates as larva and pupa in the host Toxoptera graminum Rondani. The above authors state that the adults can withstand temperature below freezing for at least two weeks in the laboratory, but may not live as long in the field, unprotected.

No specific mention of the ways of overwintering have been found in the literature for P. aguti.

Emergence. With the advent of a favorable spring environment, the imago of A. testaceipes completes its development and cuts a circular hole through the aphid cuticle just large enough for emergence (Plate 2). This hole is usually located on the postero-dorsal part of the abdomen of the host. In some instances, the lid, that has been cut off by

the emerging parasite, is left attached to the host (Sweetman, 1936). The details of emergence in the case of P. aguti are lacking in the literature. However, the emergence of P. aguti has been observed by the author and photographed (Plate 3).

The adults

Responses to environment. "The adults of A. testaceipes are most active on bright sunny days when the temperature is between 20° and 30° C. The parasites are extremely sensitive to variations in humidity: excessive dryness will kill them quickly. There is little activity among parasites on dark or rainy days or at night; at these times they rest quietly on the lower surfaces of the leaves" (Sweetman, 1936). Bilsing (1916) reports that A. testaceipes is active only when the temperature is above 13° C., while Moore (1913) comments that the parasites may be neglected as a factor in insect control below this temperature. Webster and Phillips (1912) point out that temperature and wet weather control the activity of the adults to a great extent.

Detailed observations on the influence of environment on P. aguti is lacking in the literature.

Mating. The mating habits of the two parasites are similar. The males and females mate as soon as they dry following emergence from the cocoon. Males usually take

the initiative. The actual process of copulation is often preceded by a definite courtship period. Wheeler (1923) reports that copulation lasts from 30 to 60 seconds and occurs readily in petri dishes and glass vials.

Oviposition. The habits of oviposition of aphidiine parasites have been studied by many workers. Timberlake (1910) gave a very brief account of the act in Praon simulans Provancher. Webster and Phillips (1912) described and pictured the process in A. testaceipes, and Wheeler (1923) and Spencer (1926) treated these habits of Aphidiinae in general.

The acts of oviposition by Aphidius and Praon are quite similar (Plate 2). Under favorable conditions, the females begin ovipositing within a few hours of emergence whether mated or not. The parasite approaches an aphid, arches her antennae above it tapping it a few times, and if stimulated, curves her abdomen under her head and thorax between her braced legs and elongates the abdomen until its tip comes in contact with the body of the aphid. By a sudden forceful stab a strike is performed. An egg is not always deposited. Usually only one egg is deposited in the body of the aphid, but superparasitism occurs if hosts are scarce. The egg may be placed in any part of the body of the victim, even in the head, cornicles, antennae, or the legs. If egg laying is vigorous, as on quiet, hot sunny days, aphids of

any stage beyond the first instar are attacked (Janiszewska, 1933).

The period of oviposition of A. testaceipes, according to Webster and Phillips (1912), varies from 3 days to a week or more, depending upon the temperature. In warm weather, the females live and oviposit for 5 or 6 days. A female is capable of laying 300 to 400 eggs in her lifetime (Ullyett, 1938). Laboratory studies on a species of Aphidius parasitizing Brevicoryne brassicae L., conducted at the Corunna Phytopathological Station (1937,38), showed that the adult parasites survive six to seven days without food and when fed on four per cent sugar solution live for 15 to 20 days and are able to parasitize the aphids as late as the ninth day of adult life. The adults of the third generation bred in captivity by the above station showed loss of vigor and parasitized very few aphids.

Incubation

A. testaceipes. As soon as the egg is deposited, it absorbs liquid from the body fluids of the host and increases in size enormously. During the third to fourth day, the larva frees itself from the serosa and comes to lie in the body cavity of the aphid (Sweetman, 1936). Spencer (1926) suggested that the cytolytic enzymes secreted by the developing larva, or the straightening of the larva, aid in

breaking the serosa. He believed the former hypothesis to be more probable. Only one larva develops from an egg.

P. aguti. There exists no specific mention in the literature of the incubation of the eggs of this parasite.

Larval development

A. testaceipes. There are five larval stages all of which are spent within the body of the host. During the first few stages the larva is sluggish and does not come in contact with, or cause injury to, any of the vital organs of the host. The activity is increased with age and soon vital organs are injured (Webster, 1908).

P. aguti. Observations on the development of this species are lacking in the literature. However, it may be expected that, this parasite passes through all five larval stages within the body of the host, since this is the case with other species of the same genus.

Supernumerary larvae. The occurrence and ultimate fate of supernumerary larvae in the host, due to super- or multiple parasitism, has been the subject of much controversy. Such larvae of the parasites of the genera Aphidius and Praon have been observed by many workers. Ullyett (1938) observed as many as eight larvae of Aphidius sp. developing in a single aphid, but only one reached maturity. Timberlake (1910) believed that the destruction of the extra

larvae in Praon simulans Prov. is due to chemical inhibition by the successful larva. Wheeler (1923), basing his observations on A. testaceipes, A. ribis, A. phorodontis, P. simulans, Ephedrus incompletus, and Diaeretus rapae, suggested four possibilities; namely, (a) starvation, (b) the action of a poisonous principle, (c) delicate injury by the older inhabitant and (d) accidental injury which may prove fatal later. He also added that, when the larvae are all of the same size and strength, the idea of starvation or poisoning may be impossible. Therefore, the survivor must be the one to escape injury. Spencer (1926) from observations on A. testaceipes and many other species of the same genus and on P. simulans, concluded that the inhibition is a biochemical process rather than a mechanical one since evidence of mechanical injury was never found. At present, the latter hypothesis is more generally accepted.

Attachment of parasitized hosts

It has long been known that a parasitized aphid remains in its position on the host plant long after death, until the adult parasite has emerged. Detailed contributions have been made by many workers regarding this phenomenon.

A. testaceipes. The exact manner of attachment of the dead hosts by this parasite is discussed elaborately by Kelly (1910). He states that, for a short time before the

death of the host and for 4 to 6 hours afterwards, the parasite larva can be seen through the semi-transparent host skin, engaged in making a series of revolutions. These revolutions, according to Webster (1908), probably mold the body wall of the host, while it is still plastic, into the most suitable shape for pupation. The host becomes very feeble just before death and rigidly grasps the object upon which it rests. This death grip of the host helps to hold the dead body in place while the parasite larva prepares to attach it permanently. For this purpose, the larva within makes a longitudinal slit in the venter and enlarges it into an irregular oval-shaped opening. First, the edges of the now oval slit are attached to the substratum by silk threads and emission of a glutinous fluid. By repeated additions of the adhesive materials the aphid skin is made fast.

P. aguti. Observations made on other species of this genus resemble closely those of A. testaceipes, except in a few details, as follows. The species of the genus Praon, after cutting a hole on the ventral part of the aphid abdomen, leave the host body entirely, but use it as a roof. The hole is then covered over with silk and tent-like protective walls of light layers of silk are constructed. These are connected by thin membranes and the whole serves to hold the aphid body over the parasite (Wheeler, 1923). Ainslie (1917) reported similar observations for P. simulans. Once this

protective structure is completed the larva begins to spin its cocoon.

Pupal development

As soon as the larva of A. testaceipes has attached the body of the host firmly to the substratum it begins to spin the cocoon inside the aphid skin. It takes about 20 to 26 hours to complete the cocoon (Kelley, 1910). After the completion of the cocoon, the larva becomes quiet, and in most cases assumes, according to Webster and Phillips (1912), a position directly opposite to that which it maintained during feeding and development.

In the case of Praon, the larva, after erecting the tent-like walls and after covering the emergence hole in the aphid, proceeds to spin its cocoon within them, but beneath the body of the dead host. The cocoon, which takes the form of a central capsule, is made up of the same silk as the outer walls but is packed tightly and thickly together with no intervening membranes. The cocoon is rounded-oval and of about the same size as the dead body of the host, exclusive of the legs (Ainslie, 1917; Wheeler, 1923).

The Effect of Parasitism on Host

The host is not paralysed by an ovipositional strike,

but repeated attacks produce mechanical injury. As soon as the parasite larva breaks out of the serosa, the neighboring adipose tissue of the host becomes affected. The cell boundaries become more pronounced, the cytoplasm more and more vacuolated, and the nuclei shrink and become irregular (Spencer, 1926).

An elaborate study made by Spencer (1926), on the effect of parasitization on the body systems of the host, is discussed as follows. The most obvious changes in the aphid, due to parasitism, are manifested in the reproductive system. The embryos of the host, in whatever stage they may be, are arrested in development, and large vacuolar spaces appear in them as the parasite larva grows. This brings about a degeneration and resorption of these embryos. The pseudova within the mother aphid, before initiation of their cells to form embryos, are affected only after the young and old embryos have degenerated from the effects of parasitization. The ova that develop into winter eggs are similarly arrested in development. From an economic point of view, the fact, that a cessation of the reproductive capacity of the aphid occurs on the third day, or thereabouts after parasitism, is an important consideration. The digestive system of the host may occasionally escape modification. This system, along with the muscular and nervous systems, is kept intact until late in the process of parasitization but is finally

consumed.

Ullyett (1938), basing his observations on a species of Aphidius in Africa, stated that aphids parasitized during the first two instars do not become adult; those parasitized before the end of the third instar reach adulthood but are unable to reproduce; while the number of progeny by those attacked in their later development is considerably reduced. He also stated that, owing to the relative rates of reproduction of the parasite and the host and due to the fact that some parasitized aphids are able to reproduce, Aphidius would be unable to reduce the aphid population appreciably until the aphids have passed through several generations and done economic damage, even if the parasite population was uninterrupted.

The coloration of aphids, dead from parasitism, has been a matter of interest to many workers. It is reported by Gautier and Bonnamour (1929) that species of aphids on oats parasitized by Aphidius sp. have the color of dead leaves, whereas the species collected at the same time from the same field but parasitized by Ephedrus plagiator Nees. are distinctly black. The above authors are of the opinion that the secretions or products of metabolism of the parasite larva have a profound effect on the color of the dead host. Beirne (1942) pointed out that the coloration of the dead hosts parasitized by various Aphidiinae, varies con-

siderably and is very distinctive. He added that, in the case of Ephedrus pulchellus, the aphid body takes on a dark bluish hue, while those parasitized by Aphidius matricariae Hal. are golden brown. Webster and Phillips (1912) observed that dead hosts enclosing A. testaceipes are brown in color. No specific mention regarding the color of hosts parasitized by P. aguti were found in the literature.

Rearing Techniques

Spencer (1926) reared various Aphidiinae in cages, each of which consisted of wooden embroidery hoops supported by uprights and to which was sewed a cylinder of fine-mesh cheese cloth. A square glass covered the top. The bottom of the cage was made of two glass plates which rested on the top of the pot and fitted closely around the base of the stem of the potted plant. Aphids were cultured in these cages until numerous, and then the parasites were admitted.

For obtaining parasitized aphids, Smith (1944) placed cut ends of plants, bearing aphids, in containers of water. Parasitized aphids, if any, were subsequently removed and placed in small vials covered with two layers of cheese cloth. The vials were kept over a saturated solution of NaCl which produced 74 percent relative humidity. At this humidity which Smith considered optimum for the development of the

parasites, fungi did not develop among dead parasites.

In transferring hymenopterous parasites from one tube to another, Holloway (1913) held the tubes, enclosing the parasites, mouth to mouth. This was advantageous since the parasites ordinarily go toward a source of light.

For feeding adults, Holloway (1913) suggested a weak solution of granulated sugar and water as food for the emerged parasites. This was administered by moistening the pointed end of an insect pin with the liquid and inserting it through the stopper, so as to smear some of the solution on the sides of the tube containing the adults. Many other workers suggest honey for feeding purposes (Vassiliew et al., 1914).

Evidence of Abundance and Importance

Since the utilization of the natural enemies of injurious pests has become a well established method of insect control, every phase of host-parasite association takes on economic importance. Primary parasitism is a beneficial type of association. Various primary parasites have brought successful control of pests into various regions of the world (Sweetman 1936).

Aphidius testaceipes. These parasites have done their part, with encouraging results, in several instances.

How potentially important the control exercised by them on various host aphids can be exemplified by Huxley's calculation depicting the enormous reproductive potential of these pests. Accordingly, it is postulated that, "the progeny of a single Aphis, would, in the course of ten generations, supposing all survived, contain more ponderable substance than five hundred millions of stout men; that is, more than the whole population of China".

In this country, A. testaceipes exercised control on aphid outbreaks such as the green bug, Toxoptera graminum R., outbreak of 1939 in Oklahoma (Fenton and Fisher 1940) and the cowpea aphid, Aphis medicaginis Koch. control reported by Sanderson (1906). Knight (1944) found a high degree of parasitism of the cotton aphid, Aphis gossypii Glov., in Haiti. Anderson (1912) and Moore (1913) reported encouraging results on the control of T. graminum in British East Africa. A. testaceipes is not only important in direct control of aphids destroying plant crops, but also in the indirect control exercised over the transmission of various diseases of agricultural crops. Such an example is the control of Aphis leguminosae, a vector of 'rosette disease' of ground peanuts, by a species of Aphidius (Van Der Merwe, 1931). Other examples are known and undoubtedly still others will be discovered.

Praon aguti. As these parasites have been discovered comparatively recently, records of their abundance and importance are lacking. However, other species of this genus are, in many cases, potent enemies of the aphids.

MATERIALS AND METHODS

The Host Aphids

Various species of aphids belonging to different genera were obtained from both indoor and outdoor localities. The cultures comprised the following:

1) Aphis gossypii Glov. (cotton aphis)
2) Myzus persicae Sulz. (green peach aphis)
3) " circumflexus Buckt. (crescent-marked lily aphis)
4) Macrosiphum rosae L. (rose aphis)
5) " pisi Kalt. (Pea aphis)

The identification of the first three was confirmed by the United States National Museum and the latter two by Dr. S.S. Ritchie of the Ohio State University.

The Parasites

The original specimens of Aphidius testaceipes Cresson were secured from campus greenhouses while those of Praon aguti Smith were obtained from neighboring outdoor localities and later from the departmental greenhouse. For the initial start of a population, the parasites were often collected out of doors by sweeping with a net. The parasites were identified by Dr. Muesebeck of the U.S. National Museum.

Rearing

For rearing the aphids and the parasites two types of cages were used; (1) standard battery jars, and (2) larger

cheese cloth cages built in the greenhouse. When observations were conducted with battery jars, either in the greenhouse or in the laboratory, cut stalks of the host plants bearing the insects were fitted into the necks of bottles containing water by introducing them through discs provided with a central perforation. The perforation was plugged with cotton after the plant stalk was in place. Each culture was then enclosed by the jar, the mouth of which was closed by cheese cloth held in place with rubber bands. Most of the aphids migrated within seven hours to the fresh plant material supplied at 48 hr. intervals. Transference of the remaining ones to the new stalks was done with a camel's hair brush. All hosts were kept under careful observation for at least ten days prior to the introduction of the parasites. This was done to detect and eliminate any previously parasitized hosts as well as to bring the population of the hosts to a required level comprising all different stages. Ample care was also taken to avoid mixing of different species of the aphids.

In most cases alternate host plant species were substituted for the hosts on which the aphids were first collected. This was done for the convenience of using plants well adapted to confined greenhouse and laboratory conditions. The cotton aphis, originally collected from *Hibiscus* sp., was cultured on squash (*Cucurbita* sp.),

while the peach aphis was cultured on radish (Raphanus sp.) in preference to tobacco (Nicotiana tabacum). The rose aphis was confined to rose (Rosa sp.) throughout the observations and the pea aphis was grown on peas (Pisium sativum) and on fava-beans (Vicia sp.). The crescent-marked lily aphis was cultured exclusively on wild morning glory (Convolvulus arvensis).

The parasite A. testaceipes was cultured on A. gossypii, M. persicae, and M. circumflexus, while P. aguti was cultured on M. circumflexus, M. rosae and M. pisi. The parasitized materials were handled in the same manner as described by Smith (1944). In transferring the parasites from one vial to another it was found best to hold the vials mouth to mouth, taking advantage of the fact that the parasites are positively phototropic. The feeding method described by Holloway (1913) was found very satisfactory. In instances where the parasites refused to feed, the sugar solution was replaced by plant leaves covered with honey dew of the hosts, on which the parasites fed readily.

The control of physical factors during rearing experiments is treated below in detail.

Temperature and moisture control. Experimental temperatures ranged from 25° to 34° C. For life cycle studies the parasitized specimens were kept in chambers whose temperatures were thermostatically regulated to within a small

fraction of a degree. For ovipositional strike-rate studies, appropriate temperatures were maintained by the use of electric lamps of different capacities fitted into a rectangular space made up of a wooden frame and cardboard screens covering the sides. A glass plate covered with opaque paper was placed over the frame to avoid any effect of light upon the insects. A jar cage enclosing the host plant and the insects was kept on the glass base. The temperatures were measured at different levels in the cage. Constant watch was exercised to keep the temperature nearly constant ($\pm .5^{\circ}C$). This arrangement was highly satisfactory for close observations on the habits of the parasites and hosts.

The humidity levels were attained by varying the water surface area through the use of vials of different sizes in the cages. Relative humidities were ascertained by a hygrometer. No moisture control could be exercised in the greenhouse or outdoors, but the relative humidity was measured at regular intervals throughout the days of observations.

HABITS OF THE PARASITES A. TESTACEIPES AND P. AGUTI

Mating

Only a few detailed observations have been reported in the literature on the mating habits of the parasite A. testaceipes and nothing seems to exist in the case of P. aguti. Hence the author attempted a more extensive study on such habits of the two parasites. Obviously these studies had to be conducted under confined laboratory conditions because of the extremely small size and the mobility of the insects.

First studies were aimed at determining the minimum time interval between emergence of the imagines and initial mating. Only individuals seen in the process of emergence were selected for this study. As soon as the specimens were dry and able to fly, a pair was confined in a vial and continuously observed for two hours. Of 50 pairs of P. aguti thus studied, no matings occurred within the first hour and a half of observation. But within the next half hour, in over 20 percent of the cases, matings occurred. Of 50 pairs of A. testaceipes studied, no mating took place within the first hour and twenty minutes of observation. But within the next twenty-five minutes several matings were observed. Because of the physical strain of such observations, they were discontinued after two hours. Therefore, a complete

distribution curve for initial mating cannot be constructed.

Limited studies were conducted with the unmated pairs above to determine whether or not a delay in the meeting of the opposite sexes would affect the consummation of mating. It was found that, of the 38 unmated pairs of the original 50 pairs of P. aguti, 30 mated readily, when brought together again, after an interval of about 22 hours since the first trial. The rest mated readily, when again given the opportunity, six hours later. In the case of A. testaceipes, all remaining unmated pairs of the original 50, mated, after repeated daily trials, within a maximum time interval of four days after emergence. Since all 50 pairs of P. aguti and A. testaceipes mated within 30 hours and four days respectively, it is obvious that, in general, the former species reaches sexual maturity within a day and a half, and the latter within four days.

The behavioristic pattern of mating of both species of parasites showed great similarity and was as follows. The female, prior to mating, remained motionless except for movements of the antennae and preening of the wings. As soon as the male approached her, the pair touched antennae. Afterwards, the male began moving around the female, occasionally touching her with the antennae. In response, the female moved away but the male followed until she was quiet. At this stage many instances were noticed in A. testaceipes

where the male ran over his partner five or six times, at the same time vibrating his wings rapidly. When the male secured his position on the back of the female he crawled backward, still remaining on the female's back, and bent the hind region of his abdomen downward to meet hers in copulation. This final act of copulation took an average of 52 seconds in A. testaceipes, confirming the observations of Wheeler (1923). The average time taken by P. aguti was 46 seconds. During this period the pair remained almost motionless except for the frequent touches by the male with his antennae on the body of his partner. When the process was completed, the female remained quiet for some time after the male flew off. Occasionally more than one male was seen perched on the back of the mating pair. In one instance, one female of P. aguti carried around three males one on top of the other, in addition to the mating male. Cases where males tried to mate with one another were also noticed. Such cases were observed by the author only when one of the males had just finished a successful act of copulation. Temperatures above 35° C. caused the parasites to fly restlessly about, and as a result no matings occurred. A decrease in temperature brought about an increase in the number of matings. A female of either species, once successfully mated, was not seen copulating again with the same or any other male. The actions of the male indicated

that he recognized such previously mated females. In the case of the male, multiple mating seemed to be the rule. The maximum number of matings observed for a single male of A. testaceipes during his life time was 19, all with different females. For P. aguti the maximum was 22.

It has been shown by other workers that, a relation exists between the order of mating to the sex ratio of the progeny in species of parasites. These observations on multiple matings suggested similar investigations for the species studied here. Four cases of multiple matings were observed in detail for each species. In the case of A. testaceipes, four separate males performed 15, 19, 17 and 12 matings respectively. Each male was given access to females in sequence. The pairs were isolated between times, as continuous observations were not feasible. The results, in conformity with those of other workers for other species, showed that in early matings female offspring were preponderant, and in the later ones the sex ratio of the progeny was approximately equal. The increase in the number of males from later matings may be correlated with a diminution of sperm supply in the aging male. It has been demonstrated by Whiting (1918) that virgin females of A. testaceipes occasionally produce a few females. However, in the present series of studies no females could be procured from such

virgins. Observations with P. aguti gave the same results. Here, four males mated with 20, 11, 16 and 22 females respectively. Since the sex ratio data, for all four series of matings in each species, showed remarkable similarity, it seemed necessary to give only the averages (Table 1).

Oviposition

Most of the mated females of the previous experiment, as well as some unmated specimens, were closely observed for ovipositional behavior. A female in the act of oviposition, bends her abdomen forward between her legs. This act is often preceded by the parasite tapping the back of the host with her antennae. In the case of P. aguti this was often supplemented by pressing down the aphids head with the fore legs. Generally, half-grown aphids were selected for attack. Ovipositional strikes were made on any part of the host's body but a decided preference was shown for the abdominal region (Table 2).

TABLE 1.

The Relation of Order of Mating to the Sex Ratio of the Progeny from Four Males Each of *A. testaceipes* and *P. aguti*

Female #	Average number of offspring per female			
	A. testaceipes		*P. aguti*	
	Male	Female	Male	Female
1	33	71	9	52
2	26	91	13	60
3	20	81	13	57
4	25	66	18	52
5	25	46	24	51
6	43	61	14	24
7	21	27	16	25
8	30	32	19	31
9	43	44	31	24
10	88	86	39	48
11	94	77	29	43
12	93	81	30	48
13	104	97	30	34
14	36	29	31	43
15	34	28	44	35
16	67	63	25	18
17	60	57	32	29
18	20	19	33	37
19	19	21	37	33
20			58	55
21			36	38
22			26	30
Average per female	47.6	60.6	25.8	40.5
Total off-spring	2999	3818	1781	2799

TABLE 2.

The Location of Ovipositional Strikes on Host Body
by A. testaceipes and P. aguti
(200 cases observed for each)

Position of strikes	A. testaceipes	P. aguti
Between cornicles	60	56
Sides of the abdomen	49	45
Ventral abdomen	52	57
Thorax	10	12
Leg	10	2
Through leaf	2	10
Antennae	4	2
Head	13	16

If the hosts were numerous, the parasites often struck one host after another, but with fewer hosts the same aphid might be attacked more than once, the parasite depositing more than one egg in the same host. However, the females of both parasite species generally avoided aphids that had already been successfully parasitized.

The maximum number of offspring developed from ovipositions by a single female of A. testaceipes was 254, while that of P. aguti was 230. The number of strike often exceeded the above figures. Few progeny of either parasite species were obtained from thoracic strikes. Antennal and head ovipositional strikes yielded no progeny.

Initial ovipositions by mated females of A. testaceipes under laboratory conditions, occurred four to 85 minutes after mating. For P. aguti, this interval was two to 70 minutes. Unmated females of the former laid eggs about two and a half hours after emergence, while those of the latter, about two hours after.

The total period of oviposition of A. testaceipes varied from two to ten days, while that of P. aguti ranged from approximately three to thirteen days when single females of the two species were allowed to oviposit for an hour per day (1/2 hour in the morning and in the evening). The average total number of strikes for the seven females of the former was 101.8 strikes per day, the maximum number having been accomplished on the third day (Table 3). Seven females of the latter averaged 110.2 strikes while the maximum activity was reached on the third to fifth day (Table 4).

During the progress of the aforesaid observations there was some evidence of an increase of male progeny, especially from the collection of sessiles after the seventh day of oviposition. To clarify this, 5 mated females of A. testaceipes and of P. aguti were liberated in separate cages containing their respective hosts, Myzus persicae and Macrosiphum rosae. The number of males and females that emerged from the sessiles collected from the 5th to 12th day after exposure to the parasites showed that, while the

TABLE 3

The Number of Ovipositional Strikes of Females of A. testaceipes when Allowed Free Access to Hosts for one Hour Per Day on Successive Days. (D-dead)

Females	Strikes on successive days										Total single strikes
	1	2	3	4	5	6	7	8	9	10	
1.	10	36	42	30	0	7	4	0	0	D	129
2.	14	32	41	20	9	4	1	1	D	0	122
3.	9	40	42	19	7	0	D	0	0	0	117
4.	6	14	32	10	5	1	1	1	0	D	70
5.	15	20	29	19	6	6	3	1	1	D	100
6.	10	31	33	D	0	0	0	0	0	0	74
7.	16	29	31	12	5	3	3	1	1	D	101

Total number of strikes. 713
Average number of strikes per parasite 101.8

TABLE 4

The Number of Ovipositional Strikes of Females of P. aguti When Allowed Free Access to Hosts for One Hour Per Day on Successive Days (D-dead).

Females	Strikes on successive days										Total single strikes
	1	2	3	4	5	6	7	8	9	10	
1.	7	12	0	35	31	D	0	0	0	0	85
2.	7	15	35	29	29	11	5	0	2	D	133
3.	5	10	32	48	32	9	0	D	0	0	136
4.	6	14	30	29	30	10	3	0	D	0	122
5.	7	16	27	29	28	7	0	0	0	D	114
6.	9	11	25	20	22	5	4	3	D	0	99
7.	3	11	22	21	20	0	0	5	1	D	83

Total number of strikes.	772
Average number of strikes per parasite	110.2

female offspring were numerically greater in the early collections, the number decreased more rapidly than the males. The average for parasites of each species is given in Table 5. Nevertheless, the total number of female progeny was always greater than that of the males for A. testaceipes studied. With P. aguti, the same trend was maintained on the whole, but No. 2 parasite gave forth slightly more males than females; the cause of this is unknown.

Discriminatory Instinct

It is undoubtedly true that a number of factors are involved in guiding the parasites to food and hosts. One of these is the arrangement of natural objects in organized assemblages, another is the perceptive power of the parasites, and a third is the faculty of instinct. That some parasites, and probably many, are first attracted not to a particular host but to a particular type of environment in which the host normally occurs, is well exhibited in the case of the two primary parasites A. testaceipes and P. aguti examined here.

The following experiments were conducted on the nature of reactions of the mated females of the parasites while they alighted on host plants bearing many aphid hosts and their cast skins. Five mated females of A. testaceipes were liberated successively into ten different glass cages

TABLE 5

Relationship of the Sequence of Oviposition to the Sex of the Progeny in the Case of A. testaceipes and P. aguti

Day of collection	Average per parasite					
	A. testaceipes			P. aguti		
	S	Os		S	Os	
		M	F		M	F
5.	65.	18.6	41.8	69.2	22.4	41
6.	32.4	7.2	20.8	41.8	11.6	26.6
7.	25	9.2	11.6	17.6	8	7.8
8.	4	2.2	1.4	7.2	4	1.6
9.	4	2.4	.6	6.8	3.6	1
10.	2.2	1.6	0	2.8	1.4	0
11.	1.2	1	0	2	1.4	0
12.	.8	.6	0	1.4	.4	0

Total male offspring for five females of A. testaceipes. 214
Total female offspring for five females of A. testaceipes. 381

Total male offspring for five females of P. aguti. 264
Total female offspring for five females of P. aguti. 391

S - Sessiles
Os- Offspring
M - Male
F - Female

enclosing the cotton aphis, A. gossypii, and their numerous cast skins (false hosts) under uniform conditions and their responses individually observed for 30 minutes in each cage. The same procedure was adopted for P. aguti with rose aphis, M. rosae, as hosts.

It was seen that as soon as a parasite alighted on a leaf surface bearing only the cast skins of the respective aphids, a series of searches were made over them with the antennae and in some instances by the fore legs. In some cases, the parasites even tried to assume the pose of oviposition once or twice. However, no eggs were deposited. Once the parasites had made a series of such encounters on the false hosts in the first few cages, they obviously became progressively less and less stimulated by the cast skins in the successive cages (Table 6). The total number of examinations made by a parasite, and thus, the time consumed among false hosts was finally so much reduced that, in the last three cages, practically no time was spent in scrutinizing the false hosts. Since all the females of both species of parasites responded very similarly, only the average results are given in Table 6.

From these observations two conclusions may be drawn. (1) As soon as a parasite, ready for ovipositional

TABLE 6

The Ability of A. testaceipes and P. aguti to Differentiate Between False Hosts (aphid cast skins) and True Hosts (living aphids) When Exposed Successively in a Series of Separate Cages

Cage no.	Average strikes per parasite			
	A. testaceipes		P. aguti	
	False hosts	True hosts	False hosts	True hosts
1	22.6	3.6	20.4	1.2
2	19.2	10.0	19.2	9.6
3	9.4	15.6	10.0	13.2
4	6.4	19.6	5.2	16.6
5	1.4	18.6	1.6	24.6
6	1.0	24.6	0.8	20.4
7	0.8	22.8	0.2	27.4
8	0.2	22.6	0.6	26.2
9	0	18.6	0.2	22.2
10	0	13.8	0	19.8

strikes, is given access to true and false hosts, only a small degree of stimulus (probably odor) is required to begin the process. Thus a parasite attacks cast skins in larger numbers in the first few cages. (2) As more and more eggs are disposed of, the parasite seems to require a greater intensity of stimulus, which probably only the living true hosts are able to infuse. This may explain why they progressively ignore the cast skins. It may also be presumed that the frequent trials made by a parasite on cast skins by means of its ovipositor helps the parasite to differentiate the character of the particular host required, by way of chemical stimulation exercised through the sensory cells of the ovipositor.

Further instances to support the existence of discriminatory instinct in the two species of primary parasites are dealt with in the section 'Host-Parasite Relationships'.

ECOLOGICAL RELATIONSHIPS OF THE PARASITES A. TESTACEIPES AND P. AGUTI

Abundance

Attempts were made to record the general abundance of the two parasites in three selected stations on the campus (A - Shrubby open, B - Shrubby shady, C- Grassy open with widely separated apple trees). Observations were made three days a week for the period from May to October 1954. Aphid food plants were swept with a net and the parasites counted in the laboratory. The timings of the collections were alternated between stations, one hour being spent in each. The data are shown in Table 7.

The populations of the two species of parasites were not equal in any locality during the period of the collections, except at locality C. The maximum difference existed in locality B. The population of P. aguti, in all three localities, showed remarkable similarity. While physical factors might have played a role in the gradual rise and fall of the parasite populations, the marked decrease of A. testaceipes in the locality B was obviously brought about mainly by an increase of the hyperparasite, Asaphes fletcheri Cwfd as well as by a high degree of destruction of the pupae by predators.

TABLE 7

Abundance of the Parasites A. testaceipes and P. aguti as Shown by Collections Made From May to October at Three Stations

Month	Station A		Station B		Station C	
	At	Pa	At	Pa	At	Pa
May	57	0	0	0	63	61
June	56	21	10	90	98	88
July	33	89	0	98	50	43
August	11	66	22	40	14	29
September	10	59	0	4	4	11
October	21	10	20	15	19	13
Total	188	245	52	247	248	245

At - A. testaceipes
Pa - P. aguti

Longevity of the Adults of A. testaceipes and P. aguti

The longevity of A. testaceipes was determined under three different biotic conditions, namely;

1) with hosts but no honey,

2) with honey but no hosts and

3) without honey or hosts.

The primary parasites in each of the above biotic conditions were observed under three different temperatures, 26°, 29° and 32° C. and with relative humidities of 66, 75 and 88 per cent at each temperature. Thus, a total of 27 separate tests, with 12 individuals in each, were conducted in all possible combinations of the aforesaid biotic and physical factors. The same procedure was adopted for P. aguti. The average of the data for the two parasite species is given in Tables 8 and 9.

The two species of parasites showed similar lengths of life. The average longevity of the adults of both species decreased with increase in temperature at all relative humidities in all the groups mentioned above. Hence, it is obvious that temperature alone plays a significant role in the life expectancy of the adult parasite species. Females of both species, in general, lived longer than males. Also, the maximum length of life was attained by

TABLE 8

Effect of Temperature and Moisture on Longevity of the Adults of A. testaceipes

Temperature	Average longevity in days Relative humidity 66		75		88	
	Male	Female	Male	Female	Male	Female
Adults with hosts						
26° C.	11.4	12.3	9.3	11.0	10.0	11.2
29° C.	5.2	9.2	6.5	8.5	6.4	7.8
32° C.	3.9	5.3	4.4	6.9	2.3	4.5
Adults given honey but no hosts						
26° C.	22.8	36.0	19.8	35.3	23.1	36.2
29° C.	18.1	26.7	15.3	26.6	15.5	25.4
32° C.	10.6	18.3	10.4	18.2	8.9	16.2
Adults without hosts or food						
26° C.	7.8	11.9	5.5	11.3	5.9	9.2
29° C.	5.5	8.2	3.9	8.5	4.0	6.3
32° C.	2.1	3.4	2.0	4.8	2.2	4.0

TABLE 9

Effect of Temperature and Moisture on Longevity of the Adults of P. aguti

Temperature	Average longevity in days Relative humidity 66		75		88	
	Male	Female	Male	Female	Male	Female
			Adults with hosts			
26° C.	12.1	15.2	12.6	14.5	12	13.1
29° C.	7.9	11.0	8.2	11.5	8	10.6
32° C.	3.8	4.6	3.1	4.7	4.5	5.1
			Adults given honey but no hosts			
26° C.	24.6	39.5	20.1	34.5	25.6	38.5
29° C.	17.2	30.2	15.0	27.9	18.5	29.6
32° C.	10.9	19.5	9.5	17.9	10.1	19.9
			Adults without hosts or food			
26° C.	8.0	13.3	8.2	12.1	7.8	10.2
29° C.	5.9	10.1	3.4	8.9	4.3	5.1
32° C.	2.2	4.3	2.6	4.9	2.0	3.1

both sexes when they were given honey with no access to hosts. The shortest length of life expectancy was observed among the parasites which were neither with hosts nor with honey.

Activity of the Adults of A. testaceipes and P. aguti in the field

Table 10 represents a general picture of the influence of various outdoor conditions on the activities of the parasites A. testaceipes and P. aguti. The observations are recorded in eight categories depending upon the physical conditions of the day involved. The temperature and relative humidity were recorded at the time of observations in each category. For purposes of discussion and analysis, the gradient of activity is divided into four levels, namely, active, very active, few active and very few active.

It is evident that the greatest activity of the parasites occurs on warm sunny days. Hot days restrict the activity of the parasites, as do windy days. On cloudy and hazy days with wind, there is further restriction of the activity of the parasites, resulting finally in complete inactivity. Rainy days completely obliterate parasite activity.

TABLE 10

Activity of the Adults of A. testaceipes and P. aguti in the Field

General conditions	Temperature (°C)	Relative humidity	A. testaceipes	P. aguti
Warm & sunny	29	72	very active	very active
Hot & sunny	31	88	few active	active
Haze	29	82	few active	few active
Wind & sunny	31	70	few active	few active
Cloudy	28.5	75	very few active	very few active
Rainy	28	--	none	none
Cloudy & windy	28.2	77	none	none
Haze & windy	28.5	68	none	none

Effect of Temperature on the Rate of Ovipositional Strikes by A. testaceipes and P. aguti

Observations on the rate of oviposition were conducted by the use of the equipment mentioned in the section on materials and methods. Seven mated parasites were studied individually for each primary parasite species at temperature from 25° to 32° C. at one degree intervals. Each parasite was observed while being allowed to strike numerous aphids for one hour at a specific temperature. The same method was adopted for the remaining six parasites at the same temperature with fresh groups of aphids. Table 11 gives the average number of strikes for seven parasites each of A. testaceipes and P. aguti at the temperature studied.

In the case of A. testaceipes, the maximum number of ovipositional strikes was accomplished at 29° C., while the same for P. aguti occurred at 28° C. At higher temperatures, A. testaceipes showed a greater retardation in ovipositional activity than P. aguti. For instance, at 31° C. all individuals of the former exhibited complete reluctance to attack the suitable host species unless they were artificially placed and kept among a group of hosts. Even in such instances, the parasites did not remain among the group of hosts for more than one or two minutes. P. aguti, on

TABLE 11

Effect of Temperature on the Rate of Ovipositional Strikes by *A. testaceipes* and *P. aguti*

Temperature (°C.)	Number of ovipositional strikes (Average for seven parasites) *A. testaceipes*	*P. aguti*
25	7.2	9.2
26	11.1	13.2
27	11.6	14.4
28	13	16.6
29	16.3	13
30	6	6.7
31	0	5.4
32	0	3.2

the other hand, carried on ovipositional attacks even up to 32° C. without any marked difficulty. However, the number of strikes was very low at this temperature. It was also noticed that the ovipositional strikes by both species of parasites at temperatures above the optimum resulted in very few successful emergents and these were all males. At other temperatures, on the other hand, a few males were also obtained along with a majority population of females. The aphids showed an abnormally increased activity at and above 30° C. and as a result many of the attacking parasites of either species were rendered unable to attack. Those which tried, often got caught in the exudates from the hosts. The increased activity on the part of the hosts may also partly account for the lesser number of ovipositional strikes attempted and executed by a parasite species at higher temperatures.

Effect of Temperature and Moisture on the Length of Life cycle of A. testaceipes and P.aguti

The length of the life cycles of A. testaceipes and P. aguti was found to be very similar. Thirty individuals were studied for each species under the conditions discussed below. At an average temperature of 27.6° C. and a relative humidity of 86 per cent each species required about

15 days to complete development from oviposition to emergence of the adult. At 29° C. and the same relative humidity to as low as 68 per cent, egg and larval stages together of A. testaceipes required four days and the pupa six days. The same stages in the case of P. aguti took four and eight days respectively. At 32° C. and a relative humidity of 72 per cent, the egg and larval stages of both parasites developed normally but the pupal stages of the species suffered a high percentage of mortality. This was comparatively greater in the case of P. aguti which suffered a loss of 70 per cent of the total 30 pupa as opposed to 56.6 per cent loss in the case of A. testaceipes. The pronounced effect of temperature and moisture on the pupal stages of both parasite species may be due to the fact that, the pupal stages, as opposed to the larval stages, are not bathed by the body fluids of the host, and hence are exposed, to a greater degree, to the adverse influence of the environmental conditions. The higher percentage of mortality in the pupal stage of P. aguti which passes this stage outside the body of the aphid, may be due to the greater exposure to environmental conditions.

Host-Parasite Relationships

Among the more important problems of insect parasitism, the question of host-parasite relationships deserves

considerable attention. The following discussion of the writer's observations is an attempt to express some of the more important criteria which influence the primary parasites A. testaceipes and P. aguti in selecting their hosts. Three distinct processes, host finding, host selection and host suitability, contribute to a great extent, to the determination of host acceptance of a parasite (Salt, 1938).

Host finding and host selection in A. testaceipes and P. aguti.

The ability of parasites to find their hosts varies with the species and with the environment, which is a composite of physical and biotic factors. If the physical conditions of the environment provide a suitable medium for parasite activity, logically, a parasite with an earlier ecological nitch of activity will get an earlier start than others, and hence finds more hosts. On the other hand, unfavorable physical conditions retard the speed of the process for any species and, as a result, the parasites find only fewer hosts or none at all.

In the process of host finding by a parasite, complex biotic factors also play important roles. To begin with, some parasites are attracted to the type of environment, occupied by its animal host through the influence of the food plant of the hosts. If a parasite is influenced by

the plants, the one which supplies the maximum stimulus is selected. Such is the case of A. testaceipes in Haiti, where this species is shown by Knight (1944) to be an efficient control agent of the cotton aphid, Aphis gossypii Glov. on millet, maize etc. but not of the same species of aphid infesting rubber plants. After a species of plant has been detected, the parasite may encounter many different species of hosts or a single species or none at all. Naturally, if many different species of hosts are met with, a selective ability by the searching parasite would be advantageous, since there is certain to be some variation in the degrees of adaptability of the parasite to its possible hosts. Among those hosts which supply the necessary attraction stimulus only those individuals of certain age or stage are able to arouse the instinct of attack of the parasite. This process, of elimination of a particular host species, plant or animal, in preference to some other plant and animal host that a parasite finds in a selected environment, is termed host selection. This complex phenomenon of host selection, as described above was studied in the case of A. testaceipes and P. aguti and is supported by the following observations made in the laboratory.

Plant host selection by A. testaceipes

Observations were conducted separately on large numbers of each of the following species of aphids on their

respective host plants in the greenhouse:

A. gossypii (cotton aphis) - Hibiscus and Squash

M. persicae (green peach aphis) - Tobacco and Radish

For the purpose of providing a situation for host selection under controlled conditions, the parasites were admitted into a cage enclosing two plant species bearing one host aphid species. The control tests consisted of keeping the individual plant species in two different cages to prevent a given parasite from having access to both host plants at the same time. A total of five parasites were studied with each species of aphid. These were allowed to strike for one hour per day on five successive days. The results (Table 12) are summarized as follows: the parasites, under the conditions of simultaneous access to two host plants showed a decided preference for A. gossypii multiplying on squash. However, in the control cages, the parasites performed similar number of strikes on aphids on either plant species. With M. persicae, the parasites selected, for attack, a larger percentage of hosts on tobacco than on radish, while, in the control cages, again, there was an equal amount of parasitism on the separated plant species. The above observations seem to indicate that plant hosts of the aphids have some influence on host selection by A. testaceipes. This influence may be only temporary, merely attracting the

TABLE 12

The Selective Responses of A. testaceipes to Different Host Plants of Aphids

Plant host	Average strikes per parasite					Average per parasite per day	Average of control per parasite per day
	1	2	3	4	5		
			A. gossypii				
Squash	10.4	15	17	6	3.8	10.40	23.20
Hibiscus	5.2	10.2	11.4	3.6	0.8	6.24	22.80
			M. persicae				
Radish	6	9.8	16	4.6	2.4	7.76	24.60
Tobacco	8.8	17.6	18.8	9	4.6	11.64	24.75

parasites to a likely location of hosts. If the host aphids are present, they furnish a further stimulus and the plant may be of no further influence on the parasites. Whether the same course of selection occurs, on two plants or beds of plants, in the field is unknown. Confirming the previous observations (Table 3), the maximum number of ovipositional strikes was performed on the third day.

Plant host selection by P. aguti

The influence of the host plant on selection of hosts by P. aguti was not determinable with M. rosae, since only one suitable host plant species was available. However, M. pisi was easily cultured on peas and fava beans and tests similar to those for A. testaceipes were conducted. These tests showed, in contrast to A. testaceipes, no significant difference in the selective ability by P. aguti for the two plant species tested.

Aphid host selection by A. testaceipes

This phenomenon was clarified by the following experiments conducted in a greenhouse. The parasites were given simultaneous access to the two species of aphids, M. persicae on tobacco and A. gossypii on squash. The host plants with the aphids were kept side by side in the same cage. One female parasite was liberated at a time and allowed to strike at hourly periods on five successive days. Five

parasites were studied. The results (Table 13) show that when the parasites had the availability of two different species of aphids on two different host plants, the selection was directed toward the one particular species of host which gave the greatest stimulus to the searching parasite. This explains why there was a higher number of strikes on M. persicae than on A. gossypii. On the other hand, averages for five parasites from the control data show that each species of aphid, in the absence of the other, served as an equally qualified host for the parasitic attack.

Aphid host selection by P. aguti

Experiments to this end were conducted on the same lines as those described for A. testaceipes. The hosts included M. rosae on rose and M. pisi on peas. From the results (Table 13) the following conclusions are evident. (a) When the two species of aphids were exposed simultaneously to the parasites under the same conditions, there were significantly more strikes on the former species than on the latter species of aphid, thereby showing that M. rosae was preferred. (b) When the two species of hosts were exposed to parasitism in separate cages, there were equal numbers of strikes on both species. (c) The maximum activity of the parasites, in confirmation with Table 4 and at variance with that of A. testaceipes (Table 3), occurred on the third to fifth day (Table 13).

TABLE 13

Aphid Host Selection Exhibited by *A. testaceipes* and *P. aguti*

Aphid species	Host plant	Strikes on successive days Average per parasite 1	2	3	4	5	Average per parasite per day	Average of control per parasite per day
				A. testaceipes				
M. persicae	Tobacco	6.8	17.2	18.8	6.8	3.8	10.68	24.25
A. gossypii	Squash	5.8	9.8	15.4	7.2	3.0	8.24	23.0
				P. aguti				
M. rosae	Rose	5.0	9.6	20.0	15.8	13.6	12.8	25.4
M. pisi	Pea	3.2	4.4	7.8	11.0	11.4	7.56	24.9

The above experiments draw attention to the relation of the extent of selective action by the parasite to the amount of time consumed for this process. This time may be shorter or longer depending upon the circumstances. The presence of more than one host species involves more time for selection, since the parasite is compelled to make a choice between the various groups of hosts. Then, the parasite chooses the individuals of a certain age from a selected group. It is seen in Table 13 that while one A. testaceipes accomplished an aggregate average of 18.92 strikes in the M. persicae and A. gossypii cage, the same amount of time yielded 24.25 strikes on the former and 23.0 strikes on the latter hosts in separate control cages. A single female of P. aguti made a total of 20.36 strikes in the M. rosae and M. pisi cage, while the same duration of time brought 25.4 and 24.9 strikes on the respective hosts separately. It is logical to expect some further variations in the time consumed for host selection depending upon the availability of the preferred stage of the selected host species. A comparable observation has previously been discussed under 'discriminatory instinct' (pp 46-50), where the importance of the time element is shown with respect to the selection of true hosts from a group of false hosts.

Host suitability in A. testaceipes and P. aguti

The foregoing considerations bring one to the question: if a parasite selects the hosts most suitable for the welfare of its progeny, what is the reason for; (1) the varying percentages of mortality among the developing parasites, and (2) the difference in the size or structure and abnormality in behavior of the emerged parasites?

The answers to these puzzles lie in the phenomenon of host suitability which may vary not only with the species of parasite but also with their sexes, etc. For example, Flanders (1936) has shown that some hosts may be suitable for the development of the females but not for the males of the same species of a parasite. Salt (1938) defined a suitable host species as one which generally is adequate for the development of fertile and normal parasites. He further mentioned the following features which he considered most important in estimating the degree of host suitability of host species of Trichogramma evanescens Westw. They are: (a) the host species must be suitable for attack,

(b) for the eggs to be laid

(c) for the development of the immature stages, and

(d) for the imago to emerge.

However, the present studies on A. testaceipes and P. aguti suggest that even when the above requirements are satisfied

by a host population in general, under uniform conditions, there may be few to several hosts in the same population which do not necessarily comply with all four requirements. Such an exhibition of unsuitability by some hosts of a generally suitable group of hosts at present can only be presumed partly due to the differential influence of environmental conditions, unless a complete physico-chemical and biological discription of the hosts concerned are made. This latter analysis of the hosts is not attempted at present.

Host suitability in A. testaceipes

It has been concluded previously (pp. 66-67) that this parasite, when selecting hosts for ovipositional strikes, chooses M. persicae on tobacco in preference to A. gossypii on squash. If the former species thus selected by the parent parasite should serve as suitable host of the highest order, the requirements, b, c and d mentioned before have still to be fulfilled. That this is not always the case is shown by the following discussion of the data in Table 14.

It is apparent that the average number of strikes made by a parasite in five days is decidedly greater on M. persicae than on A. gossypii. Hence, from the viewpoint of suitability of attack, the former species of host has secured the higher rank. But, when the average number of sessiles procured from such strikes is considered, it be-

comes obvious that a parasite lost 9.7 per cent of its young either as egg or larva in M. persicae, while in A. gossypii there was a reduction of only 3.8 per cent. The unsuccessful cases may have been due to any one or a combination of the following causes: (1) unsuccessful strikes with no deposition of egg by the parent; (2) failure of egg to develop and, (3) failure of larva to complete its development. Considering the question of the number of progeny emerged from the respective sessiles, there was a loss of 23.5 per cent individuals in M. persicae while in A. gossypii the loss was only 9.09 per cent. On the whole, there was a total loss of 31.08 per cent offspring in M. persicae and 12.6 per cent in A. gossypii.

Briefly, then, a greater loss occurred in M. persicae. This suggests, that A. gossypii while comparatively less suitable for the attack of the parasite, was more suitable than the former for development of the immature stages of the parasite. This throws light upon the fact that certain advantages exhibited by a particular host for meeting one of the specific needs of a parasite may be counter-balanced by deficiencies of the same host toward some other developmental needs of the same parasite. This factor should be an important consideration when these parasites are employed in the field, and it is to be understood before hand, that

even though they may prove as efficient agents to suppress the number of pests initially with almost 'explosive rapidity' as Clausen (1951) has put it, the matter of maintaining a dependable population throughout the season may present an entirely different situation.

A third species of aphid, Myzus circumflexus, which was subjected to the attack of A. testaceipes showed marked unsuitability in all requirements. When this species was caged with M. persicae or A. gossypii, it was relatively infrequently chosen for ovipositional strikes. Of the several specimens of Myzus circumflexus which received the strikes, only a very few resulted in successful emergence of the parasites. These emerged parasites seemed to lack the discriminatory instinct while selecting hosts for attack. Further, the manner of attack of such individuals, on many occasions proved detrimental not only to the reproduction of their progeny but to themselves, since the latter often became fatally entangled in the exudate from the cornicles of the hosts. Details of these observations are treated in a later section 'Conditions governing host suitability' (pp 82-91).

P. aguti

It was shown earlier (Table 13) that M. rosae served as the most preferred host for the ovipositional strikes by

P. aguti. To determine the character and extent of suitability, the same procedure as adopted for A. testaceipes was undertaken. The average results, in Table 14, show that M. rosae not only was suitable for the attacks of the parasites but also for the development of the progeny. This is illustrated by the following observations.

(a) Each parasite lost, on the average, 4.06% of its progeny as egg or larva in M. rosae, while in M. pisi, the loss was 8.9%.

(b) Of the sessiles of M. rosae, there was a loss of 15.9%, while of M. pisi there was a loss of 16.2%.

(c) The total percentage loss of progeny in M. rosae was 19.37%, and in M. pisi 23.8%.

Experiments with M. circumflexus produced the same kind of results as those discussed with regard to A. testaceipes. Details of these experiments are considered along with A. testaceipes in the section 'Conditions governing host suitability' (Pp 82-91).

The general conclusions arrived at are, that A. testaceipes and P. aguti seem to possess a marked degree of instinctive ability to select the 'general conditions' suitable for them and their progeny; whereas their ability to select the 'specific or particular conditions' suitable seems more circumscribed. In other words, if the parasites, studied here, always possessed the capacity to select the

TABLE 14

Host Suitability in *A. testaceipes* and *P. aguti*

Host	Average per parasite (for five days) Strikes	Sessiles	Progeny
	A. testaceipes		
M. persicae	53.4	48.2	36.8
A. gossypii	41.2	39.6	36.0
	P. aguti		
M. rosae	64.0	61.4	51.6
M. pisi	37.8	34.4	28.8

'specific or particular conditions' suitable for them, usually there would have resulted, for each ovipositional strike, one progeny. But this is an unusual occurrence in the life of any organism, because many factors, which appear stable in the beginning of a process of selection, may frequently take an unfavorable turn making the most favorable individual for development into a very unsuitable one. This conclusion is in agreement with Thompson (1939) who emphasized that even an intrinsically reasonable behavior of a parasite may be frustrated due to certain accidents that may be brought about by the 'laws of nature'. He stressed that "the proportion of suitable conditions in the environment are always low, and because it is, organisms die in large numbers at random, because the environment though not unorganized, varies qualitatively and quantitatively in the details of its structure from moment to moment, and from place to place, in a way that must be ascribed to chance".

Physical conditions governing host finding and host selection by A. testaceipes and P. aguti

The general behavior of the parasites in selecting the proper hosts and the requirements for labelling a host as fit for selection and finally suitable have already been discussed. With this information at hand, attempts were

made to determine the influence of certain environmental factors on the aforesaid phenomena.

Light

That light did influence the host finding ability of the parasites was shown by the following observations in the laboratory and in the field.

a) At night, when temperature and humidity were kept at the same level as during the day the parasites preferred to rest on the sides of the glass cage or on the cheese cloth covering the mouth of the cage, even in the presence of preferred stages of the preferred host species.

b) This nighttime inactivity was always reversed when sufficient light was provided, under favorable temperature conditions.

c) On cloudy days the parasites were less active, even when temperature and humidity were as high as on sunny days.

d) Under controlled conditions in the laboratory, a greater percentage of strikes was effected on hosts that remained in an area of higher light intensity.

e) Further increase in the light intensity often resulted in promoting activity among the parasites.

f) After a certain number of strikes was performed by the parasites, a majority of them flew toward the source of light.

Temperature

Under outdoor conditions, the parasites were very active on warm sunny days with temperatures around 28° to 29° C. and relative humidity from about 70 to 90 per cent. Their great activity under these conditions very probably enabled the parasites to find a larger percentage of hosts than otherwise. Studies on ovipositional strikes in the laboratory indicated that A. testaceipes possessed a shorter temperature range of activity than P. aguti (Table 11). Above 32° C. the parasites were abnormally active and continuously attempted to escape. Under such extreme conditions of temperature, the parasites did not show any tendency to seek or select host species.

Humidity

The effect of humidity on the parasites was evident from observations in the field. As already shown (Table10), the parasites were not seen in the open on rainy days. On hot dry days the parasites usually occupied the under surface of the leaves regardless of the location of hosts. This might have been due to the higher level of moisture at such locations.

Generally, the parasites are efficient in controlling the aphids, if the latter occur in conditions favorable for the activity of the parasites. Thus, the author observed

that a drop in parasite activity produced, for example, by rainy weather provides a chance for the host to multiply and retain a numerical superiority. Such a condition has also been reported by Anderson (1912) and Moore (1913) showing that the aphid hosts, in general, are able to breed well as low as 10° C., and are not greatly retarded until a mean temperature below 5° C. is reached; whereas the activity of A. testaceipes ends completely at 14° C.

Sometimes even when all physical conditions are favorable, host finding and host selection appear to be quite abnormal. Thus, some hosts that are normally selected by the parasites are ignored at times, and, some hosts, including those seldom selected and comparatively unsuitable for the development of the progeny, are selected at times. The first phase of the above problem has been discussed (pp 63-69), in the analysis of the stimulus produced by the host plants and aphids on the searching parasites. The second phase is discussed below. Numerous crescent-marked lily aphids, M. circumflexus, were cultured on morning glory and subjected to the attacks of the mated females of A. testaceipes and P. aguti. These parasites had been kept aloof from any species of hosts for about eight hours after their mating and before liberation into the cages enclosing the plants bearing M. circumflexus. Since the maximum rate of ovipositional

strikes of the two parasites had been determined to occur at 29° C. and 28° C. respectively, the observations were conducted at these temperatures. A total of seven parasites of each were studied individually for one hour. The number of ovipositional strikes which the two species of parasites attempted or accomplished on the hosts are shown in Table 15.

A high percentage of strikes was accomplished on new born hosts, a stage unsuited for the development of both parasites in any aphid host. These new born aphids were often selected for attack especially if they remained in close proximity to the mother. Probably odor is one of the criteria promoting such attack. Strike attempts on alate host did not give rise to any progeny, and in many instances, the attacking parasites were rendered helpless due to the effect of the exudates from the cornicles of the host in which they were entangled. The massiveness of the alate hosts as well as the interference of the wings of such hosts seemed to be the reason why the attacking parasites failed to fulfill their aim successfully. Only attacks on apterous adults gave forth successful emergents, and these were only very few, while attacks on new-born, half-grown and alate adults produced no offspring.

Although such a preponderance of unsuitable hosts

TABLE 15

The Number of Ovipositional Strikes by A. testaceipes at 29° C. and P. aguti at 28° C. on Myzus circumflexus

Host stage	Average percentage of strikes A. testaceipes	P. aguti
New born	44.9	46.03
Half grown	5.8	10.30
Alate adult	3.7	4.40
Apterous adult	45.3	39.10
Total strikes by seven parasites	238	202
Average per parasite	34	28.8

may not be of general occurrence in nature, these observations suggest that under certain circumstances, even well qualified parasites are at times compelled to accomplish only their immediate demands. Presumably, the reason underlying this phenomenon is the compelling urge these parasites have to dispose of the numerous fertilized eggs, which have been stored in their bodies since mating. As a result, when these parasites are liberated among a group of hosts in cages, their habits deviate markedly from a discriminatory disposition to a random pattern. In such circumstances the number of strikes of the parasites often exceed that which they perform in the same interval and under the same optimum temperature when normal conditions exist. Thus, A. testaceipes, made an average of 34 strikes in M. circumflexus (Table 15), after an extended denial of access to the hosts, while with normal access to A. gossypii, the preferred hosts, a normal number of strikes (average 16) was made (Table 11). In the case of P. aguti the respective strikes under the two different conditions were 28.8 and 16 (Tables 15 & 11).

Conditions governing host suitability in A. testaceipes and P. aguti

The fact that conditions of the environment vary quantitatively and qualitatively from place to place and

from moment to moment has been emphasized by many investigators. This being true, it is possible that some hosts, which have been considered previously as suitable for the parasites A. testaceipes and P. aguti under certain physical conditions, may be less suitable, or completely unsuitable, under some other environmental conditions. Thus, a species of host showing suitability at one location may or may not do so at another locality.

Apart from the influence of the physical conditions, there are biotic factors which influence suitability. These factors are extremely important for labelling a host as suitable or unsuitable for a parasite. It has already been mentioned that M. circumflexus showed a marked degree of unsuitability for the development of the parasites A. testaceipes and P. aguti. Although physical conditions play their part in the process of suitability, in the case of M. circumflexus they were of lesser importance than the biotic ones because this species was seen to be unsuitable for parasitism under the same conditions in which A. gossypii and M. rosae were suitable for A. testaceipes and P. aguti respectively. With these facts in mind, the author undertook a series of experiments which are discussed below.

Five parasites of A. testaceipes reared from M. circumflexus were allowed to attack the hosts, M. persicae

and A. gossypii. Individual parasites were allowed access simultaneously to both species of hosts for an hour on each of five successive days. The same procedure was adopted for P. aguti reared from M. circumflexus on its hosts M. rosae and M. pisi. The number of strikes by each parasite species on its two accessible host species was carefully observed and recorded under the optimum temperature conditions. The relative humidity was 85 per cent during all observations. The number of sessiles obtained from the strikes as well as the number of progeny emerging from the sessiles were recorded. The control groups for each daily test consisted of M. circumflexus serving as hosts for the parasites reared from this same species.

The results recorded in Table 16 show that the number of strikes made by these two species of parasites developed in M. circumflexus was low when compared to that made by the same species of parasites which developed in their respective suitable hosts (Table 13). Further, it was also seen that the number of sessiles was reduced by half or more, while the reduction in number of emergents was still greater. These facts show that the parasites reared from M. circumflexus cannot perform parasitization successfully in any species of host tested. The cause of such inefficiency may be due to the inadequate development that

TABLE 16

Degree of Parasitism Accomplished by A. testaceipes (A.t) and P. aguti (P.a) Reared from M. circumflexus, on the Same (control), and Other Hosts

	Control		Totals for five parasites in five days			
			A.t		P.a	
	A.t	P.a	M.p	A.g	M.r	M.s
Strikes	20	29	24	22	27	17
Sessiles	10	18	6	6	12	6
Progeny	4	9	2	4	4	1

M.p - Myzus persicae
A.g - Aphis gossypii
M.r - Macrosiphum rosae
M.s - Macrosiphum pisi

these striking parasites had undergone while developing in very unsuitable hosts such as M. circumflexus. Thus, suitability of conditions which the above mentioned species of aphid offered for the development of the parasites A. testaceipes and P. aguti was lower than in the case of A. gossypii or M. rosae.

This idea is further supported by the following experiments. Here, the parasites studied belonged to two groups. In the case of A. testaceipes, (a) ten parasites were reared from M. persicae, out of which five were allowed to strike A. gossypii and five to strike M. circumflexus, (b) ten were reared from A. gossypii, out of which five were allowed to strike M. persicae and five to strike M. circumflexus. In the case of P. aguti, (a) ten were reared from M. rosae out of which five were employed to strike M. pisi and the rest to strike M. circumflexus, (b) ten were reared from M. pisi, out of which five were allowed to strike M. rosae and the rest to attack M. circumflexus. These experiments were conducted in the same way and under the same physical conditions as those described for the preceding experiments.

The results (Tables 17, 18, 19 & 20) show that for A. testaceipes, in all instances, M. persicae served as the most suitable host species for the ovipositional strikes

TABLE 17

Degree of Parasitism Accomplished by A. testaceipes Reared from M. persicae, on the Same (control), and Other Hosts A. gossypii and M. circumflexus

	Control	Average for five parasites Hosts A. gossypii	M. circumflexus
Strikes in five days	56	47.6	48.2
Sessiles	50	45.2	13.6
Progeny	38	41.4	3.8

TABLE 18

Degree of Parasitism Accomplished by A. testaceipes Reared from A. gossypii on the Same (control) and Other Hosts M. persicae and M. circumflexus

	Control	Average for five parasites Hosts M. persicae	M. circumflexus
Strikes in 5 days	48	51	44
Sessiles	48	46.8	9
Progeny	46	40.6	2.8

TABLE 19

Degree of Parasitism Accomplished by P. aguti reared from M. rosae, on the Same (control), and Other Hosts, M. pisi and M. circumflexus

	Control	Average for five parasites Hosts	
		M. pisi	M. circumflexus
Strikes in 5 days	56	48	41.4
Sessiles	54	40	17
Progeny	48	33	4.8

TABLE 20

Degree of Parasitism Accomplished by P. aguti reared from M. pisi, on the Same (control), and Other Hosts, M. rosae and M. circumflexus

	Control	Average for five parasites Hosts	
		M. rosae	M. circumflexus
Strikes in 5 days	48	53.4	34.6
Sessiles	45	50.8	12.8
Progeny	35	46.6	4.2

regardless of the parasite's origin. Compared to the number of strikes, the number of sessiles and progeny resulting from A. gossypii were proportionately greater than those resulting from M. persicae. All M. circumflexus, in successive tests, received an almost equal number of ovipositional strikes, and the number of sessiles and progeny resulting from such strikes were much reduced, showing low suitability.

In all cases of P. aguti, the maximum number of ovipositional strikes was performed on M. rosae. This host maintained its suitability for complete development of the offspring. M. pisi showed a lesser degree of suitability for all the requirements of the parasites. M. circumflexus, as in A. testaceipes, received a nearly comparable number of strikes but the number of sessiles and progeny resulting from such strikes was low.

Thus, M. circumflexus, in all instances, proved deficient in the qualities required to make it a suitable species. Nevertheless, it must not be forgotten that if this species had been cultured on plant hosts other than morning glory, the results might have been different.

Effect of parasitism on hosts

The phenomenon of insect parasitism frequently results in the degeneration of one of the participants in

the process, and this participant is usually the host. The effects of parasitism on or in a host species are manifested in many different ways depending upon the parasite and the host involved. In the case of aphids parasitized by A. testaceipes or P. aguti, the main effects of parasitism are exhibited in three different but consecutive categories. They are, (1) effects of oviposition, (2) effects of development of the parasite larva on the structure of the host species and (3) the ultimate effects due to parasitism resulting in death and change in color of the host species. Based primarily on present studies, each of these categories are separately discussed below for A. testaceipes and P. aguti.

Effect of ovipositional strike on host behavior. All aphid species struck by either parasite species showed a to and fro motion lasting for some time. Renewed attacks produced a marked degree of sluggishness on the part of the host species and apparently stimulated them to eject copious quantities of exudate through the cornicles. New-born aphids often succumbed to multiple attacks sooner than mature ones. In the case of P. aguti, some attacks resulted in upsetting the equilibrium of the host species, and as a result, these hosts were seen hanging to the host plant by means of their beaks.

Structural modifications of the host. If a host species is parasitized preceding the third instar, it will not mature. On the other hand, an aphid species, if successfully parasitized after it had reached the reproductive stage, ceases reproducing when the parasite larva reaches the third stage, and subsequently stops feeding. As the parasite larva reaches the fourth stage, the digestive and nervous systems of the host are also attacked. Similarly, the muscular system of the host body is also finally consumed. However, the muscles of the appendages are left intact, probably due to their inaccessibility to the parasitic larva. Very soon the host becomes moribund. The sessile stage of the host, parasitized by A. testaceipes or P. aguti, is reached several hours after its death.

Before the host becomes sessile, the parasite larva of both species are seen to make a number of revolutions within the host body. These revolutions, in the case of A. testaceipes, according to Webster and Phillips (1912), round out the host body and make it more spacious for passing the pupal stage of the parasite. Since P. aguti passes its pupal stage beneath the body of the dead host, (Plate 4) the rounding out of the host body cannot serve the aforesaid purpose. These revolutions are probably concerned with ingestion of host remains and fluids by the parasitic larva.

Coloration of the parasitized host. In general, an aphid species enclosing an advanced stage of either parasite species shows abnormal coloration. For example, Webster and Phillips (1912) state that as soon as the larva of A. testaceipes reaches maturity, the aphid abdomen becomes yellow. This coloration becomes more intense and more conspicuous as the host becomes sessile. Present studies show, however, that the coloration of a sessile host is not constant for either parasite species. For example, specimens of rose aphids parasitized by P. aguti were pearly-white in color after becoming sessile on the rose plant, but some specimens which happened to become sessile on a brown surface were pale brown in color. Similarly, cotton aphids remaining sessile on hibiscus after parasitization by A. testaceipes were much darker in color than those of the same species on squash.

PART II

THE HYPERPARASITE, ASAPHES FLETCHERI (CRAWFORD)

Part II

THE HYPERPARASITE ASAPHES FLETCHERI CRAWFORD

ANALYSIS OF LITERATURE

Taxonomy

The taxonomic status of the hyperparasite A. fletcheri Cwfd. has undergone many changes since its original treatment. The hyperparasite was first described by Crawford (1909) under the name Megorismus fletcheri and was included in the family Miscogasteridae by Viereck et al (1916). The family Miscogasteridae was replaced by the tribe Lamprotatini (Muesebeck, et al, 1951). However, Kloet & Hincks (1945) gave this tribe, the rank of a family (Lamprotatidae). The genus Megorismus was transferred to the family Pteromalidae and the genus Asaphes Walker (1834) was substituted for it (Muesebeck et al, 1951). Megorismus thus became a synonym of the genus Asaphes. Recently, Burks (correspondence 1954) stated that americana, described by Girault in 1914, is a synonym of fletcheri.

Incidentally, it seems necessary to indicate that Kirby (1837) introduced the genus Asaphes in the family Elateridae of the order Coleoptera. However, this can not be considered a valid name because the genus Asaphes, erected by Walker (1834), has priority.

Description

Adult. Crawford (1909) gave the following description. "Female. Length, 1.50-1.75 mm. Bronzy green; abdomen black, obscurely bluish or greenish; antennae black, scape metallic; face in front of ocelli smooth, polished, the rest of the head reticulated; head and thorax with sparse long hairs, each set in a puncture; thorax reticulated, posterior margin of prothorax, parapsidal areas laterally, and scutellum back of the transverse furrow, smooth; metathorax rugose, with a short median carina and a smooth space on each side near the base; wings yellowish, nervures honey-color; coxae metallic, the rest of the legs testaceous; petiole stout, longitudinally rugose; abdomen smooth. "Male. Length, 1.50 mm. Similar to female; the flagellum, however, light brownish".

Griswold (1929) figured the immature stages (Plate 5) and described them as follows.

"The Egg. The egg is pearly white in color and oval in outline, although it is somewhat more rounded at the anterior than at the posterior end. Upon measuring 10 eggs they were found to average about 0.25 mm. in length and 0.1 mm. in width.

"The larva. The early instar larva is more or less top-shaped, the anterior end being quite blunt while the posterior end tapers somewhat. As development progresses,

the caudal end fills out and finally the larva becomes crescent-shaped, thus differing entirely from the larvae of either Aphelinus jucundus or Aphidencyrtus inquisitor.

"The pupa. The newly formed pupa is pale yellow in color, but soon the eyes become brownish-orange, then the body gradually darkens until it has become almost black. The pupa, like the larva, is crescent-shaped and lies on its side in the body of the dead aphid".

Distribution

The hyperparasite A. fletcheri has been reported in North America by Muesebeck et al, (1951) from the following places.

Ontario, Quebec, Connecticut, New York to North Carolina and Kentucky, and north to Iowa and Wisconsin. Massachusetts should also be added to the list.

Hosts

Many aphids as well as other primary parasites are listed as hosts of A. fletcheri (Muesebeck et al, 1951 & others). The inclusion of aphids as primary hosts suggests that A. fletcheri may act as a primary, but more likely is due to failure to differentiate the exact sequence of parasitic attack.

Muesebeck et al (1951) give the following species

of aphids and parasites as hosts for this hyperparasite.

Aphids. Anuraphis bakeri (Cowen)
Anuraphis roseus Baker
Aphis rumicis L.
Aphis sorbi Kltb.
Eriosoma lanigerum (Hausm)
Kakimia houghtonensis (Troop)
Macrosiphum cornelli Patch
Macrosiphum pisi (Kltb.)
Myzus persicae Sulzer
Periphyllus negundinis (Thos.)

Parasites. Aphidius phorodontis Ashm.
Aphidius polygonaphis Fitch
Aphidius testaceipes Cress
Aphelinus jucundus Gahan
Aphelinus semiflavus How.
Aphidencyrtus aphidivorus (Mayr)
Diaeretus rapae (Curt.)
Praon simulans (Prov.)

Biology

The recorded knowledge of the biology of A. fletcheri is very scanty.

Hibernation. There is no information in the literature on the over wintering habits of this hyperparasite.

Emergence. According to Spencer (1926), the adult A. fletcheri emerges from the aphid body through an irregular circular hole that differs considerably from the smoothly cut emergence hole of Aphidius. The location of the hole, according to Griswold (1929), is not constant. She found that 83 per cent of the emergence holes on the posterior end of the dead body of the host and that only a single adult emerges from each aphid.

Responses of adults to environment. Griswold (1929) stated that the adults are very active fliers. Further details concerning the effect of environment on the activity of the adults, are lacking.

Mating. Spencer (1926) stated that "mating occurs as soon as the female is dry". According to Griswold (1929), copulation in A. fletcheri is always preceded by "a sort of courtship". She noted that in this act of courtship, a male jumps on the back of a female and stands there, his fore legs grasping the female's eyes, and the hind legs resting on her wings. The female walks about carrying the male on her back but no actual mating is reported to have been observed. Since Griswold did not actually observe mating it is difficult to interpret her observations.

Oviposition. Spencer (1926) conducted detailed observations on the ovipositional habits of A. fletcheri. According to him, oviposition can occur with or without fertilization. For oviposition, the female of the hyperparasite locates a sessile aphid containing a late larva or early pupa of Aphidius or other primary host. Only a parasitized aphid, in which the host larva has spun its cocoon, is selected for attack. Aphid after aphid may be investigated by A. fletcheri with her delicate antennae until an acceptable one is found, and then the wasp climbs upon the aphid skin, squats a little, points her antennae downward and

starts drilling with the ovipositor. It takes about five minutes constant work for the egg to be deposited. Griswold (1929) confirmed Spencer's observations. The hyperparasite according to Griswold, places the egg on the outside of the host parasite larva within the aphid body. Generally only one egg is laid on a host, but in one instance she found three eggs of A. fletcheri on one parasite larva. Whether these eggs are the results of a single attack of a parasite or multiple attacks by the same parasite or three different parasites was not determined by Griswold.

Incubation. The incubation period requires four days (Griswold, 1929).

Larval development. The larva, according to Spencer (1926), is very active while developing as an ectoparasite on the primary. It normally remains attached near the middle of the host, sucking out the host body fluids. Griswold (1929) noted that after the primary larva had been consumed, the hyperparasite remained about 11 to 12 days in the larval stage.

Pupal development. The pupal stage is passed within the aphid body and lasts about five to six days. Thus, the entire life cycle extends over a period of approximately three weeks (Griswold, 1929).

Economic Importance

Practically no primary parasite species escapes the attacks of hyperparasites. Insect hyperparasites have often seriously interfered with the successful employment of primary parasites. The hyperparasite A. fletcheri, being in no way deficient in the destructive characteristics of a typical hyperparasite, can greatly impede man's utilization of the primary parasites A. testaceipes and P. aguti. The literature contains no statistical data to show the exact extent of hyperparasitization by A. fletcheri on the above primary parasites. Nevertheless, reports of the occurrence of this hyperparasite in various regions, warrant careful investigation. Griswold (1929) suggested that A. fletcheri may act either as a secondary or tertiary parasite depending upon circumstances. In the latter event, if preference is shown for other secondary parasites such as Charipes sp. which is secondary on Aphidius sp., then A. fletcheri, a tertiary parasite, could be considered beneficial.

MATERIALS AND METHODS

Aphids and Primary Parasites

Cultures of aphids and primary parasites were obtained employing methods described in Part I.

Hyperparasites

The original specimens of *Asaphes fletcheri* Crawford were obtained from neighboring localities by the following methods; (1) sweeping with a hand net for the adults and (2) collecting hyperparasites in the laboratory from material obtained from outdoors. The hyperparasites were identified by B.D. Burks of the U.S. National Museum.

Rearing

Mass rearing of the hyperparasites on the immature stages of the primary parasite *Aphidius testaceipes* was conducted in cages in the greenhouse and laboratory. For this purpose, the adults of *A. fletcheri* were admitted into the cages enclosing the host plants bearing aphids parasitized by *A. testaceipes*. Only a limited number of hyperparasites could be reared from the other primary parasite *Praon aguti*. After hyperparasitization of the host within the dead aphid, the aphid was transferred from the plant into a small bottle and kept at uniform temperature and humidity.

The moisture in sealed rearing jars was controlled with saturated salt solutions. Three saturation deficiencies 3, 8, and 15 mm. were maintained at each of three temperatures, 23, 27 and 30° C. respectively. Table 21 gives the salts used to obtain these saturation deficiencies at the above experimental temperatures.

The 27° and 30° C. temperatures were maintained in constant temperature chambers, and the 23° C. temperature in a circulating water bath that provided a jar temperature of 22.2° to 23.8° C. with an average temperature of 23° C.

Studies on oviposition were conducted along the same lines as discussed in Part I. The adult hyperparasites were handled and fed in the same manner as the primary parasites.

TABLE 21

Saturation Deficiencies Employed and Salts Used to Obtain Them

Temperature	Saturation deficiency (approximate) (mm. of mercury)	Salt
23° C.	3	Potassium chloride
	6	Ammonium nitrate
	15	Magnesium chloride
27° C.	3	Sodium potassium tartrate
	6	Potassium tartrate
	15	Cobalt chloride
30° C.	3	Copper chloride
	8	Sodium nitrate
	15	Sodium nitrite

HABITS OF THE HYPERPARASITE ASAPHES FLETCHERI

Mating

Fifty newly emerged pairs of A. fletcheri were observed to study the habits of courtship and mating. Of the above, 15 pairs failed to court or mate throughout their lives while the rest began courtship after an average time interval of 68 minutes after emergence. The courtship, which preceded copulation with 29 pairs, lasted an average of four minutes, while the remaining pairs courted intermittently but did not mate. These observations confirm the statement of Griswold (1929) that courtship precedes mating. However, since Griswold did not observe mating, her interpretation of what constitutes courtship may have been in error.

During the act of courtship, the male exhibited vigorous movements of his antennae and wings. He stood face to face with the female and began tapping her antennae with his. At times he circled around and occupied a position behind her and touched her abdomen with his antennae. Meanwhile, the female remained passive except for slight movements of her antennae. Suddenly after a brief pause in the activity of both sexes, the male jumped on the back of the female, grasped the sides of her body with his hind

pair of legs, the middle pair resting on her wings while the fore pair clasped her head from the sides. The female frequently fluttered her wings slowly before raising her abdomen to meet that of the male in copulation. The twenty-nine pairs remained in copula for an average period of about 15 seconds. Often two or three males were seen courting a single female simultaneously. Usually the first male to mount the female succeeded in mating with her. In one instance however, a male which climbed on a female's back soon after another male had established himself on her, succeeded in dislodging the former and performed copulation.

A male is capable of mating with more than one female. How many times a female mates during her lifetime in nature is unknown. In the laboratory, a female, once successfully mated, was not seen approached further by males any more. Mated females gave forth mostly female progeny, while unmated females produced only males. It was also seen that the number of progeny of unmated females was less than that of the mated females (Table 22).

Oviposition

In general, the hyperparasites were ready for oviposition as soon as they became dry following emergence. Mating was not a prerequisite to oviposition. If mated, the females began oviposition after a minimum average mating

TABLE 22

Sex Ratio of the Progeny Produced by Four Pairs and Four Unmated Females of *A. fletcheri*

	Number and sex of progeny			
	Mated		Unmated	
	Males	Females	Males	Females
	12	60	50	0
	2	88	58	0
	11	49	66	0
	10	53	37	0
Total	35	250	211	0
Weighted percentage of sexes	12.2	87.7	100.	0

time of 45 minutes. If a newly emerged pair was enclosed with parasitized aphids which had turned brown, the female hyperparasite did not respond to courting but proceeded with oviposition. If the pair was kept together with no access to any hosts or with access to living aphids or aphids that had not turned brown but enclosed the developing primary parasite larva, the female responded immediately to the courting approaches of the male.

The process of oviposition by A. fletcheri was always preceded by a careful examination of each aphid which may or may not have enclosed the primary parasite larva. This examination took 10 to 15 minutes. During this time, a female of A. fletcheri sought an aphid skin which enclosed a late larva or early pupa of the primary parasite A. testaceipes. Only an aphid skin which had turned brown after primary parasitization was selected for attack. The hyperparasite moved around such an aphid often touching the latter with the antennae. After palpating the aphid with her antennae, the hyperparasite mounted the dead aphid body enclosing the immature primary parasite. She stood with her antennae pointing down before the final act of oviposition. The ovipositional process took more time than and differed considerably in its behavioristic pattern from the primary parasites. First, the female, after squatting a little, began drilling through the aphid skin with her

ovipositor. When the skin was penetrated, the ovipositor was slowly pushed in apparently to locate the primary parasite, before laying an egg. It took an average of six minutes to complete the drilling and egg laying processes. These observations did not reveal multiple attacks by a single female A. fletcheri on one host or more than one female on the same host.

The female A. fletcheri showed an overall preference of attack for A. testaceipes to P. aguti. Among A. testaceipes, the hyperparasite selected for attack about 50 per cent more of the early pupal stage than of the late larval stage. In the case of P. aguti, the preference was in the reverse direction and there was a more conspicuous discrimination between the stages involved than in the case of A. testaceipes (Table 23). Details of this selective behavior of the hyperparasite are dealt with in a separate section,'Host Relationships of A. fletcheri'(pp 119-122).

The total period of oviposition of A. fletcheri varied from a minimum of two days to a maximum of 13 days when the hyperparasites were allowed to oviposit for only two hours per day. The maximum number of ovipositional drillings occurred on the first day, decreasing rapidly for three or four days but continuing at a low level till the thirteenth day (Table 24). Perhaps the longer period of oviposition

TABLE 23

Proportion of Host Stages Selected for Ovipositional Drillings by A. fletcheri

Parasite	Host stage: Late larva A.t	Late larva P.a	Early pupa A.t	Early pupa P.a
1	12	5	20	0
2	14	9	26	2
3	0	5	12	1
4	10	6	13	0
5	13	8	21	3
Total	49	33	92	6

A.t - Aphidius testaceipes
P.a - Praon aguti

TABLE 24

Rate of Ovipositional Drillings by A. fletcheri on Aphids Enclosing Early Pupa of A. testaceipes, When the Former was Given Access to the Primaries for Two Hours per Day

P	Rate of oviposition on successive days													Totals for 13 days
	1	2	3	4	5	6	7	8	9	10	11	12	13	
1	17	11	0	10	2	2	2	2	0	0	0	1	1	48
2	12	5	8	0	4	3	1	1	1	1	0	0	0	38
3	8	6	6	3	0	0	0	0	0	0	1	0	1	27
4	15	10	6	1	0	0	1	1	1	1	0	0	0	36
5	11	10	0	0	3	1	1	1	0	1	1	0	0	29
6	15	12	0	0	0	0	0	0	0	0	0	0	0	27
Total for 5 parasites	78	54	20	14	9	6	5	5	2	3	2	1	2	

P.- Parasites

in A. fletcheri, as compared to the primaries, may be due to the smaller number of ovipositions performed per day. The latter in turn may be due to the longer time consumed by the hyperparasite in effecting an oviposition. If this is the case in the field also, many primary parasites are bound to escape the assaults of A. fletcheri.

ECOLOGICAL RELATIONSHIPS OF THE HYPERPARASITE A. FLETCHERI

Abundance

The general abundance of the hyperparasite A. fletcheri was determined in the same three localities and under the same routine as for the primary parasites A. testaceipes and P. aguti.

A comparison of the data in Table 7 and Table 25 suggests that the marked reduction of A. testaceipes in locality B may have been due primarily to the greater abundance of A. fletcheri in this locality. This reduction in the population of A. testaceipes indicates that, in the field, the hyperparasite prefers the former primary parasite to P. aguti. Further, the seasonal curve of abundance of A. fletcheri follows more closely that of A. testaceipes than that of P. aguti, thereby indicating again a preference for the former primary parasite.

TABLE 25

Abundance of the Hyperparasite A. fletcheri as shown by Collections Made From May to October at Three Stations.

Month	Station A	Station B	Station C
May	0	2	2
June	30	10	65
July	31	66	10
August	8	25	7
September	0	1	0
October	4	0	3
Totals	73	104	87

Field studies showed the final reduction in number of A. fletcheri in a locality was due to the absence of suitable hosts for hyperparasitization. As a result, no hyperparasites could be collected from the said locality. However, they were obtained from other neighboring localities at the same time, suggesting a migratory habit of A. fletcheri.

Longevity of the Adult A. fletcheri

Under laboratory conditions, when supplied with numerous hosts and enough honey as food, the female hyperparasite lived for about 24 days: the males lived a few days less. Without honey or hosts, the sexes lived for about 6.2 and 3.1 days respectively.

Effect of Temperature on the Rate of Ovipositional Attempts by A. fletcheri

The influence of temperature on the rate of ovipositional attempts by A. fletcheri was studied by the use of the same equipment as that used for the primary parasites. At each temperature, 26°, 28°, 30° and 32° C., ten mated hyperparasites were individually given access to fresh groups of sessile aphids enclosing the immature stages of A. testaceipes.

The maximum number of ovipositional attempts occurred at 28° C. (Table 26). The highest number of attempts at any temperature was very low, as compared to that performed

TABLE 26

Effect of Temperature on the Rate of Ovipositional Attempts by A. fletcheri

Temperature (°C.)	Average number of attempts by ten parasites
26	7.1
28	9.5
30	6.0
32	3.0

by either primary parasite species. This, as indicated before, may be due to the longer time consumed by A. fletcheri in effecting an oviposition. However, as opposed to the primary parasites, A. fletcheri did not show as wide a variation in the number of ovipositional attempts at different temperatures. Although the number of attempts at 32° C. was lower than that at the optimum, the number was almost equal to that of either primary parasite species. This may be due partly to the fact that the hyperparasite is not handicapped by the movements of its hosts, as is the case with the primary parasites. Of the ovipositional attempts observed in this experiment, 85 per cent resulted in the production of female offspring.

Effect of Temperature and Moisture on the Length of Life Cycle of A. fletcheri

The length of the life cycle of A. fletcheri from the deposition of egg to the emergence of adult was determined at temperatures of 23°, 27° and 30° C. Three saturation deficiencies, 3, 8, and 15 were used at each temperature. In every such temperature-moisture combination 12 hyperparasites were studied.

The effect of temperature, (Fig. 1), is shown by the fact that the length of life cycle decreases with an increase in temperature. From the approximate zones of development shown in the figure, it is also seen that at 30° C. the No. 1 zone is shifting toward an environment which is more moist at 3 and 8 mm. saturation deficiencies than at 15 mm., thus, suggesting the influence of moisture on the life cycle. Also, the length of life cycle of males, in all conditions, was shorter than that of the females. The hyperparasite differed from the primary parasites at all conditions, as the egg and larval stages required more time than the pupal stage. For example, at 27° C. and a saturation deficiency of 15 mm., (i.e. 47.5 per cent relative humidity approximately), the egg and the larval stages consumed 11.2 days in the case of the males and 11.9 days in the case of the females. This was more than double the time consumed by the primary parasites. Although the

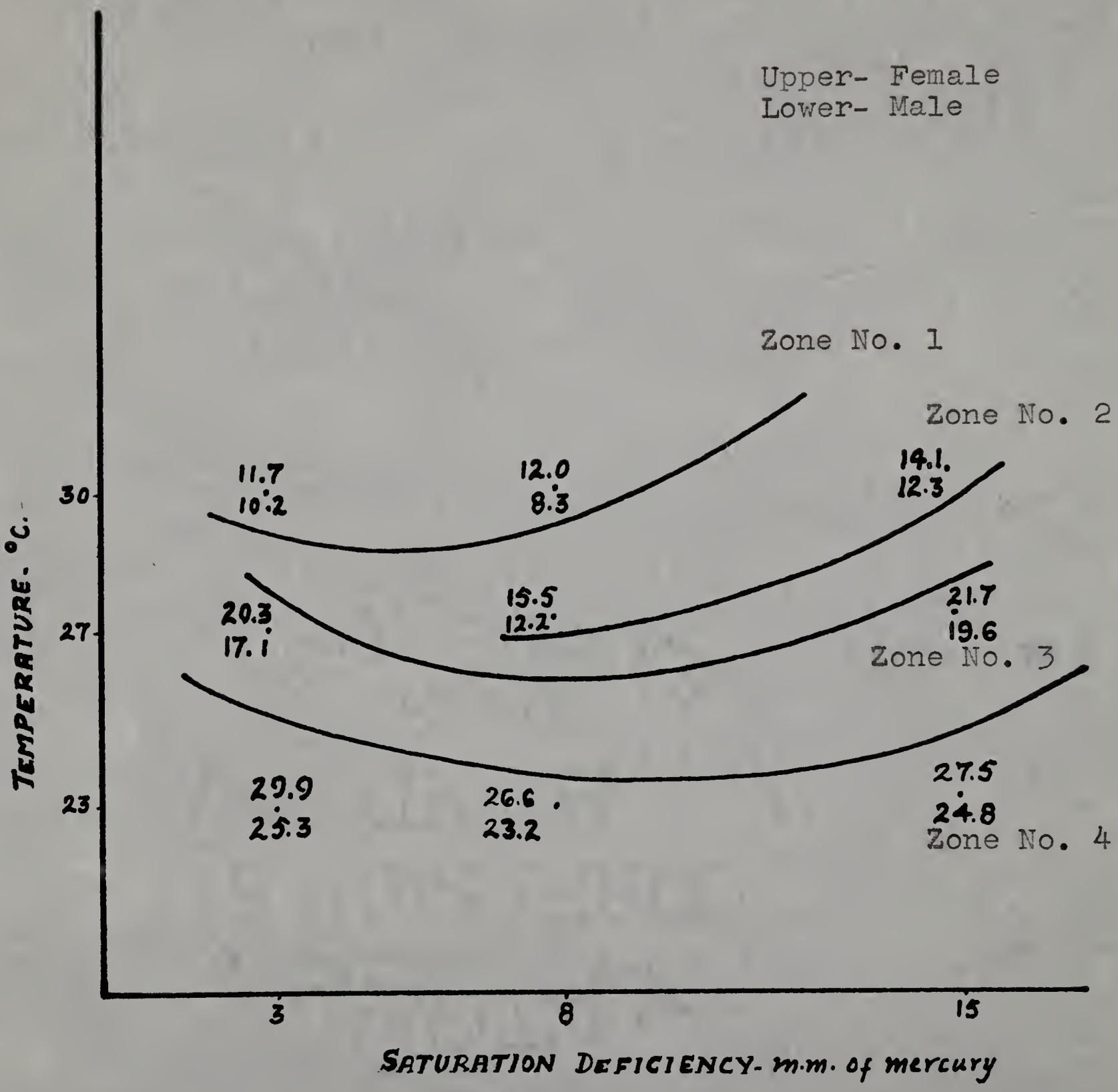


Fig. 1 Effect of Temperature and Moisture on the Length of Life Cycle of A. fletcheri

length of the egg and larval stages in both males and females of A. fletcheri was about equal, the pupal stage of the females lasted slightly longer than the same stage of the males under all conditions.

Host Relationships of the Hyperparasite A. fletcheri

Like the primary parasites, the hyperparasites have, in general, certain requirements which must be fulfilled by various host species. Just as there are many factors that check the undue increase of primary parasites, so also, there are factors preventing the excessive increase of hyperparasites. These factors, according to Muesebeck and Dohanian (1927), are "the lack of sufficient hosts in available situations, because of previous excessive parasitism or destruction by other means; the habits of the adults of most species of feeding at the puncture holes made by the ovipositor, and so rendering many parasitic hosts unfit for sustaining hyperparasite larvae; competition among hyperparasites for the same host, tertiary parasitism, enemies such as rodents, birds, predatory insects that destroy primaries and hyperparasites by feeding upon them, climatic factors, etc. All these and many others combine to maintain, in the long run, the proper relation between hyperparasites and primary parasites".

The aforesaid factors were found, in general, appli-

cable to A. fletcheri. However, careful observations did not show any host feeding tendency among the several hyperparasites.

Host selection by A. fletcheri

In general, hyperparasites are less discriminatory than primary parasites regarding the selection of hosts (Muesebeck et al, 1927). While this conception may be largely true, there are exceptions to the rule. For example, A. fletcheri exhibits a marked degree of discrimination while selecting suitable host species. It had been established by Spencer (1926) and Griswold (1929) that A. fletcheri would attack only sessiles aphids. This observation was confirmed by the present author.

Two other phenomena, establishing the existence of a high development of discriminatory instinct of the hyperparasite, also came to light in the present study. The first, also observed by Spencer (1926), is that A. fletcheri will attack only the late larval or early pupal stages of A. testaceipes. Present studies on ovipositional attempts of A. fletcheri not only confirmed this as a possibility, but also brought to light the second fact that the hyperparasite definitely shows preference for just one of the aforesaid immature stages of A. testaceipes or P. aguti.

The above conclusions are based on the following

experiments. Five hyperparasites were individually studied with a population of each of the primary parasites. (1) Fifty sessile aphids containing A. testaceipes with equal numbers of late larval and early pupal stages were exposed to hyperparasitization simultaneously. One hyperparasite was allowed to attack during two hours daily for five days. (2) A second group of each primary parasite, consisting of 25 individuals of each of the aforesaid stages was exposed to attacks of A. fletcheri separately, one hour daily for five days.

When the two stages of A. testaceipes occurred together, the percentage of attacks effected on sessile aphids enclosing early pupal stages was 89.2 per cent as opposed to 35.6 per cent on the late larval stages (Table 27). With P. aguti, the preference was in the reverse direction, with 21.2 per cent of attacks on late larval stages and 4.8 per cent attacks on early pupal stages. When the two stages of A. testaceipes were exposed to attack separately, 96 per cent of the early pupal stages and 41.2 per cent of the late larval stages received attacks. These observations show that the hyperparasite prefers the early pupal stage over the late larval stage of A. testaceipes. With P. aguti, when the stages were separated, the late larval stage only was attacked and the number of attacks was a little higher than that occurring on the same stage when the two stages

of this parasite were attacked simultaneously. This shows that the late larval stage of P. aguti is preferred over the early pupal stage.

The second phenomenon indicating a high development of discriminatory ability is that the hyperparasite attacks a much higher percentage of A. testaceipes than P. aguti (Table 27). This confirms the field observations that A. testaceipes is preferred over P. aguti.

TABLE 27

Discrimination of Hosts and Host Stages by A. fletcheri When (1) two stages (25 each) of Each Primary Were Attacked Simultaneously for Two Hours and (2) Each Stage Attacked Separately for one Hour

	Average attempts per hyperparasite in five days			
	A.t		P.a	
Stages	LL	EP	LL	EP
(1)	8.9	22.3	5.3	1.2
(2)	10.3	24.2	7.3	0

A.t - Aphidius testaceipes
P.a - Praon aguti
LL - Late Larva
EP - Early Pupa

SUMMARY

Part I. The Primary Parasites *A. testaceipes* and *P. aguti*

The primary parasites, *A. testaceipes* and *P. aguti*, are endoparasites of various species of aphids. During the present study, the former was cultured in *Myzus persicae* Sulzer, *Aphis gossypii* Glover and *Myzus circumflexus* Buckton; the latter in *Macrosiphum rosae* Linneus, *Macrosiphum pisi* Kaltenbach and *Myzus circumflexus* Buckton.

In the laboratory, the earliest mating among newly emerged pairs of *A. testaceipes* occurred in not less than 1 hour and 20 minutes after emergence. In the case of *P. aguti*, the same took place in not less than 1 1/2 hours after emergence. When kept together 2 hours per day, all pairs of *A. testaceipes* under observation had mated within a maximum time interval of 4 days after emergence and all of *P. aguti* within a day and a half. Actual mating in all cases was preceded by courtship. The act of mating in *A. testaceipes* and *P. aguti* averaged 52 and 46 seconds respectively. Females were seen to mate only once in their lifetime. Multiple matings seemed to be the rule with the males. A definite correlation between the order of mating and the sex of the progeny was observed in both parasite species. Mated females produced male and female offspring

while unmated ones males only.

Fertilized females of A. testaceipes started oviposition in 4 to 85 minutes after mating and of P. aguti in 2 to 70 minutes. Unmated females of the former species laid eggs about 2 hours and 30 minutes after emergence, whereas those of the latter about 2 hours after emergence. The process in both species took only a fraction of a second. Half-grown and unparasitized aphids were usually chosen for attack. Preference was shown toward striking in the abdomen of the host species. When placed with hosts 1 hour per day, the maximum ovipositional activity of A. testaceipes was observed on the third day and that of P. aguti on the third to fifth day. The maximum number of offspring developed from ovipositions of a single female of A. testaceipes was 254 and from P. aguti 230. The number of strikes often exceeded these figures. The sessiles from early ovipositions by a single female produced more female offspring than males, but the number of female progeny decreased more rapidly than the males as ovipositions advanced.

The population density of A. testaceipes varied at different localities on the campus. That of P. aguti showed considerable uniformity. There was scarcity of A. testaceipes in one locality where the hyperparasite Asaphes fletcheri was abundant.

The two primary parasite species had similar lengths of life. The average longevity of the adults of either species decreased with increase in temperature at all relative humidities studied. Females of both species lived longer than males. The maximum length of life for either sex of A. testaceipes was attained at 26° C. and a relative humidity of 88 per cent when the parasites were offered honey but no hosts. The maximum length of life of males of P. aguti was reached at 26° C. and a relative humidity of 88 per cent, and that of the females at the same temperature with a relative humidity of 66 per cent when the parasites were given honey but no hosts. The shortest length of life of males of A. testaceipes occurred at 32° C. and a relative humidity of 75 per cent, and that of females at the same temperature with a relative humidity of 66 per cent when either sex had neither hosts nor food. In the case of P. aguti, the longevity of the males and females was shortest at 32° C. and a relative humidity of 88 per cent when either sex lacked hosts and food.

The greatest activity of the parasites occurred on warm sunny days. Hot days restricted the activity of the parasites as did windy and hazy days. On cloudy and hazy days with wind there was further restriction of the activity of the parasites resulting finally in complete inactivity. Rainy days completely obliterated parasite activity.

The lengths of life cycle of the primary parasites were similar. At 27.6° C. and a relative humidity of 86 per cent, either species required about 15 days to complete the life cycle. At 32° C. and a relative humidity of 72 per cent, the egg and larval stages of both species developed normally but the pupal stage suffered a high percentage of mortality. This was greater in the case of P. aguti than in A. testaceipes.

The instinct of discrimination was highly developed with both primary parasites. They readily distinguished between false (cast skins) and true hosts. While selecting true hosts for attack, the parasites showed a greater preference for one group of host species over another. Only individuals of certain age were usually selected for attack. All the hosts selected were not necessarily suitable for the development of the offspring. Physical and biotic factors influenced the above-mentioned processes of host finding, host selection and host suitability in the case of both primary parasite species. Among physical factors, light, temperature and humidity were very significant. M. persicae on tobacco in the case of A. testaceipes, exhibited maximum stimulus for attack while A. gossypii on squash exhibited maximum suitability for development of offspring. With P. aguti, M. rosae exhibited greater

stimulus for attack as well as greater suitability for development of offspring than M. pisi on pea and fava bean. M. circumflexus on morning glory satisfied the least number of requirements for both species of parasites. Those individuals of either primary parasite that developed in M. circumflexus lacked the ability to discriminate between hosts.

Aphids struck by either parasite species exhibted a to and fro motion lasting for some time. Repeated attacks produced sluggishness in adult hosts. New-born aphids succumbed to multiple attacks sooner than adults. Host species attacked before the third instar did not reach maturity whereas those parasitized after having attained the reproductive stage ceased reproduction when the parasite larva of A. testaceipes or P. aguti reached the third instar. Vital organs of the hosts were attacked when the larva of either species of parasite reached the fourth instar. The color of sessile hosts was not constant for either parasite species.

Part II. The Hyperparasite *A. fletcheri*

The hyperparasite *A. fletcheri* is a secondary parasite on *A. testaceipes* and *P. aguti*. In the laboratory, *A. fletcheri* was cultured on both species of primary parasites.

The hyperparasites courted before mating. The courtship began after an average time interval of 68 minutes after emergence and persisted for about 4 minutes. The act of copulation required an average of 15 seconds. Each male was capable of mating with more than one female. Mated females were completely unattractive to males. Fertilized females produced mostly female progeny while unmated ones only males. The progeny of unmated females were fewer than those of mated females.

In general, the hyperparasites were ready for oviposition as soon as they became dry after emergence. If mated, females started oviposition after a minimum average mating time of 45 minutes. Newly emerged females in the company of suitable hosts did not court or mate but proceeded with oviposition. The deposition of an egg required an average of 6 minutes. The total period of oviposition ranged from a minimum of 2 days to a maximum of 13 days when the hyperparasites were allowed to attack 2 hours per day. The maximum number of attacks occurred on

the first day of liberation.

The increase in population of A. fletcheri in the field coincided with a marked scarcity of A. testaceipes especially in one locality where both A. testaceipes and P. aguti were present. This suggests that in the field A. fletcheri preferred A. testaceipes over P. aguti.

Maximum longevity of the hyperparasites was observed when they were given food but no hosts. Females lived longer than males. The maximum number of eggs deposited was made at 28° C.

The life cycle of A. fletcheri required a maximum of about 27 days at 23° C. with a saturation deficit of 3 mm. and a minimum of about 10 days at 30° C. with a saturation deficit of 8 mm. Males required less time to complete the cycle than females. Temperature and moisture had a significant influence on the length of the life cycle.

Like the primary parasites, A. fletcheri showed a marked degree of development of discriminatory instinct to select hosts. Only sessile aphids were selected for attack. Among A. testaceipes, A. fletcheri preferred the early pupal stage while with P. aguti the preference was for the mature larval stage. The degree of discrimination between the stages of P. aguti was more sensitive than that for the stages of A. testaceipes. On the whole, a greater percentage of hyperparasitization was accomplished on A. testaceipes than on P. aguti.

Plate 1

Developmental stages of A. testaceipes

(After Webster and Phillips, 1912)

1. Adult female and antenna of male greatly enlarged.

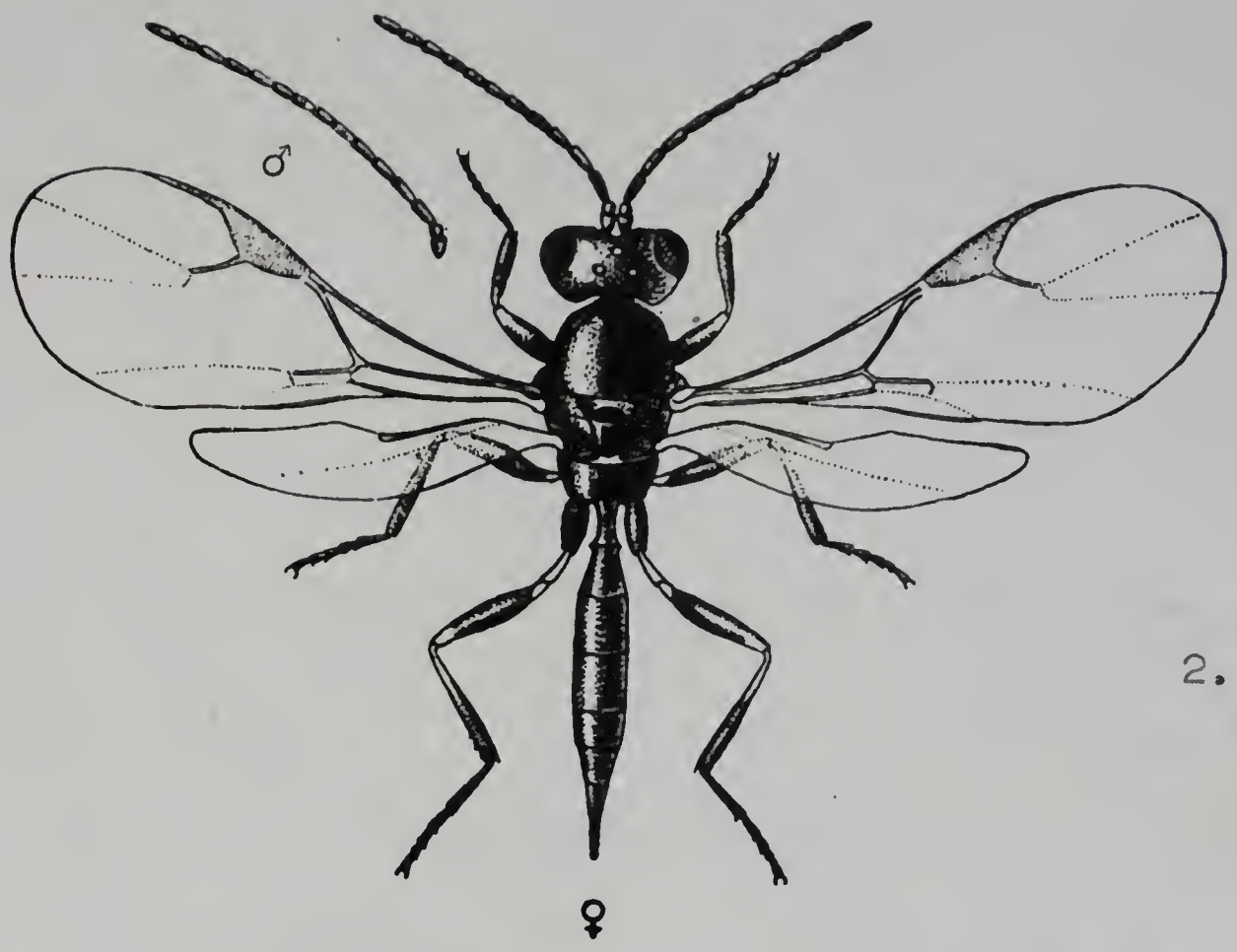
2. Egg highly magnified.

3. Full grown larva much enlarged.

4. Full grown larva
   a) Lateral view just prior to pupation.
   b) Front view of head.

5. Pupa immediately after pupation.

PLATE -1-



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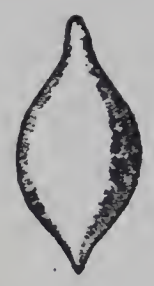

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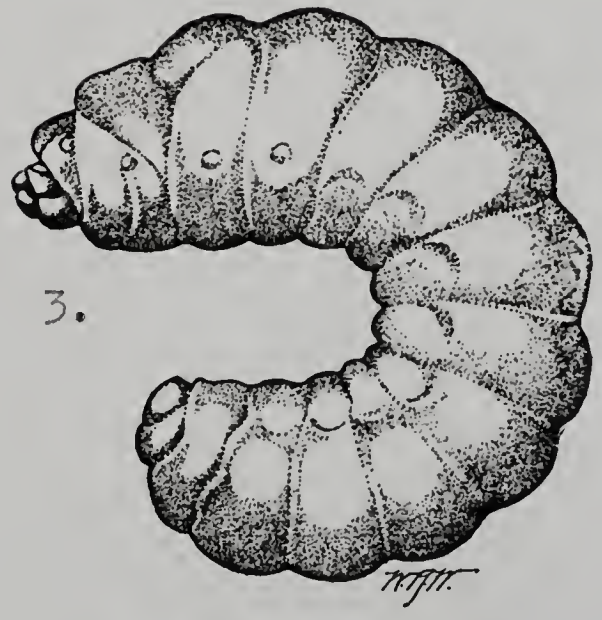

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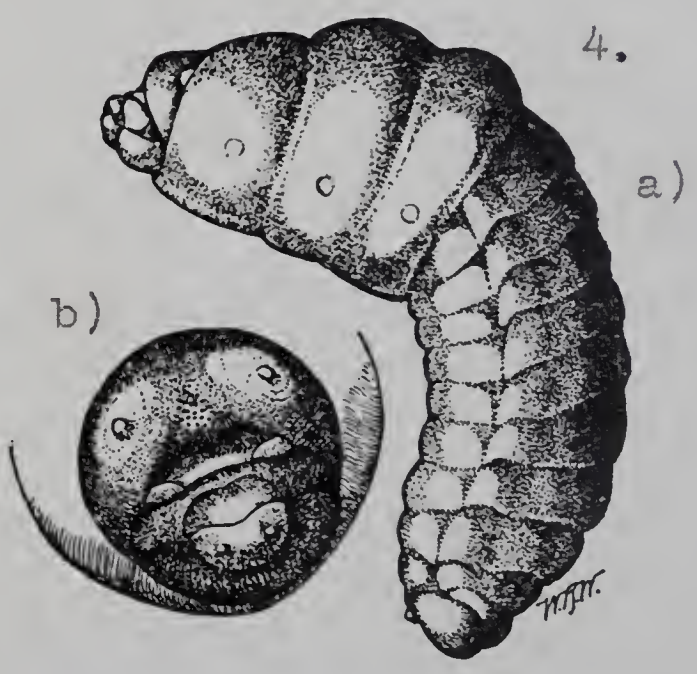


4.

a)

b)

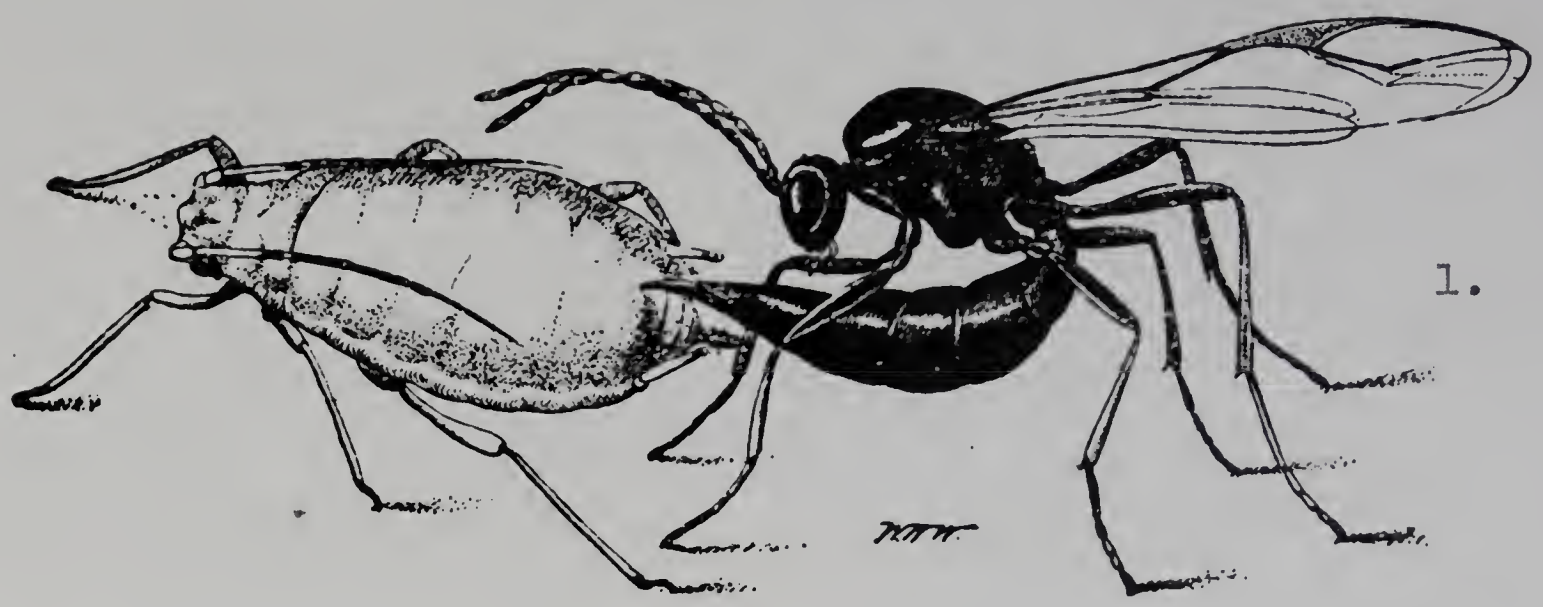
5.

Plate 2

1. Act of oviposition by A. testaceipes
   (After Webster and Phillips, 1912).

2. Dead aphids showing emergence holes of A. testaceipes.
   (After Webster and Phillips, 1912).

PLATE -2-



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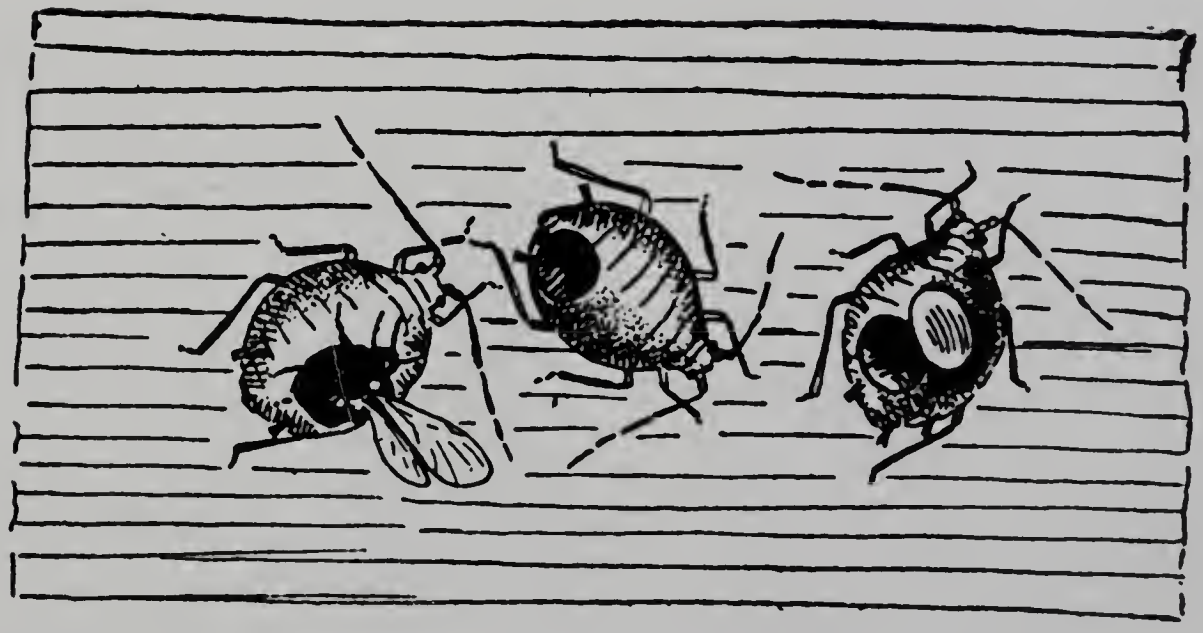


2.

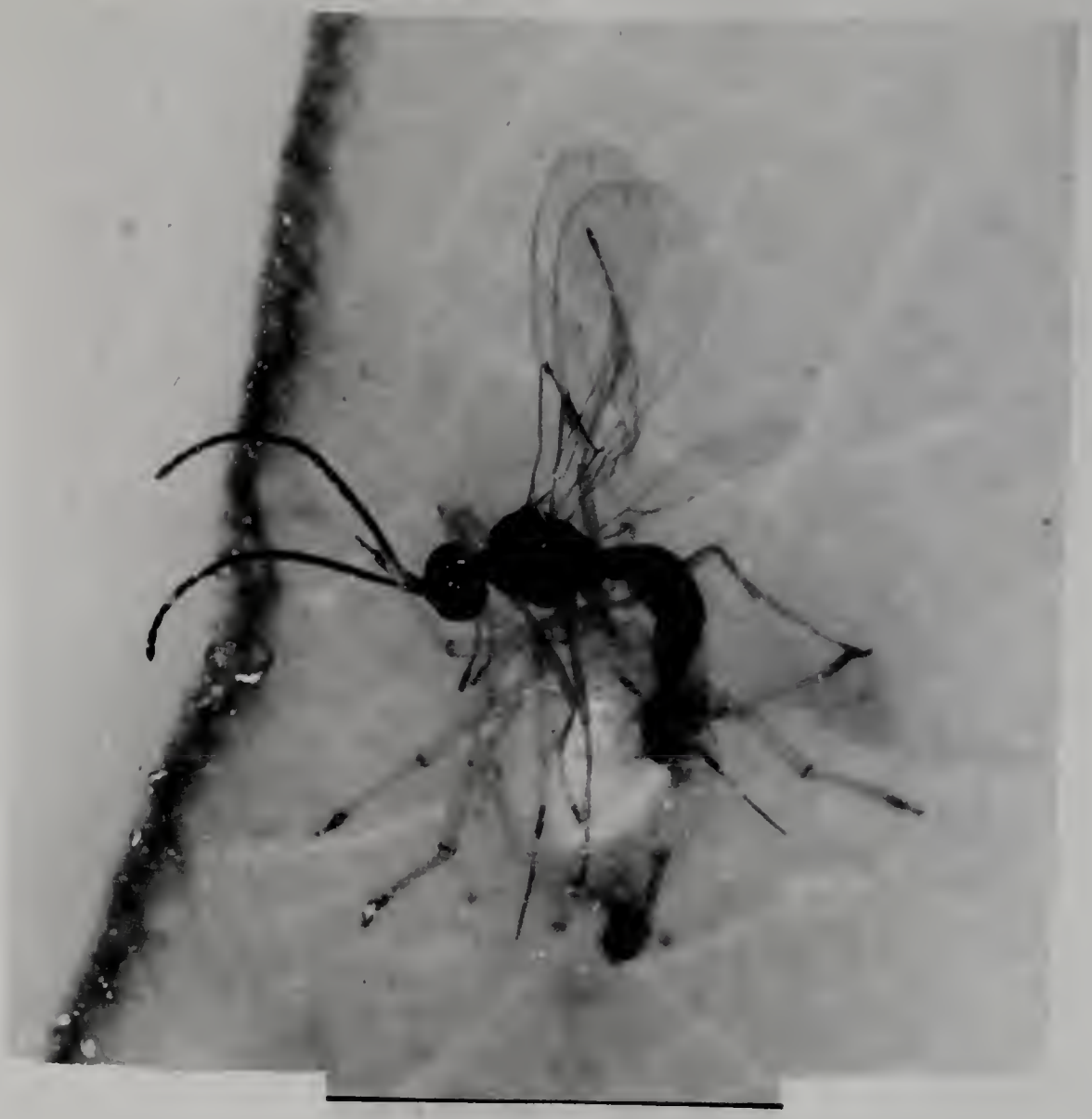
Plate 3

P. aguti

1. Adult emerging from a dead aphid (Original)

2 & 3. Pupae (Original)

PLATE -3-



1.

2.

3.

Plate 4

Effects of parasitization on rose aphids (*M. rosae*) by *P. aguti*. (Original).

1. Apterous rose aphids before the effects of parasitization become evident.

2. The same aphids after the parasitic larva has spun the cocoon beneath.

PLATE -4-

1.

2.

Plate 5

Developmental stages of A. fletcheri
(After Griswold, 1929).

1. Egg
2. Mature larva, lateral view.
3. Pupa, lateral view.
4. Adult male.

PLATE -5-

1

2

3

4

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